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JOURNAL
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ARNOLD ARBORETUM

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STUDIES OF THE EUPHORBIACEAE, PHYLLANTHOIDEAE II. THE AMERICAN SPECIES OF PHYLLANTHUS DESCRIBED BY LINNAEUS

GRADY L. WEBSTER

DURING THE COURSE of monographic studies of *Phyllanthus* L. and its near allies, it has become necessary to determine the identity of the species described by Linnaeus in order to typify the various genera. This is the more urgent, as the circumscription of a number of genera and subgenera in this subfamily will have to be modified. In this paper I wish to consider only those New World species of *Phyllanthus* described by Linnaeus and to correct, where possible, the misinterpretations they have undergone. The remainder of the Linnaean Phyllanthoideae offer their own special problems which will be dealt with later.

The investigation of the nomenclature of Linnaean *Phyllanthus* has been laborious, and the original draft of this paper could not have been written without the assistance of Drs. Richard A. Scott and Richard S. Cowan, who photographed and examined for me critical specimens at the British Museum of Natural History and at the Linnaean Society. Since then, with the cordial assistance of Mr. William Stearn and Mr. A. H. G. Alston of the British Museum and Mr. O'Grady of the Linnaean Society, I have been able to examine personally the collections in the herbaria of Linnaeus, Miller, Plukenet, and Sloane.

Linnaeus first referred to *Phyllanthus* in the "Systema Naturae" (ed. 1, 1735), where it appears as *Diasperus*, without a description. Otto Kuntze (Rev. Gen. 2: 599–601. 1891), following his extreme principle of strict priority, transferred some four-hundred-odd species of *Phyllanthus* to *Diasperus*, but this was rendered illegal by the decision of later botanical congresses to adopt the "Species Plantarum" as the starting date for genera. In the first edition of the "Genera Plantarum" (1737), Linnaeus adopted the name *Phyllanthus* and thereafter maintained it in the same sense.

In the "Hortus Cliffortianus" (1738) * appear for the first time three

* This book is dated "1737" on the title-page, but appears not to have been issued that year. Cf. Smith, Select. Corr. Linnaeus 2: 308 (1821), where Linnaeus in his

American species of *Phyllanthus*. The first species, which in the "Species Plantarum" (1753) appears as *P. epiphyllanthus* L., is the one from which Linnaeus took the generic name. The plant was first listed by Paul Hermann (Parad. Bat. Prodr. 365. 1689) * as *Phyllanthos americana planta, flores e singulis foliorum crenis proferens*. Linnaeus cited Hermann's work, but did not credit the genus to him in the "Genera Plantarum" (1737), perhaps because the latter did not provide a generic description.

Commelin (Hort. Med. Amstelodam. Rar. Pl. 199–200, *pl. 102*. 1697) provided an excellent illustration which leaves no doubt that the plant in question is the same as the one interpreted today as *P. epiphyllanthus*; the spirally arranged simple lanceolate phylloclades positively distinguish this species among the representatives of sect. *Xylophylla*. Furthermore, the specimen in the "Hortus Cliffortianus" Herbarium represents the same species, although it most likely was collected in the Bahamas, while Commelin's plant came from Puerto Rico.

Unfortunately, Linnaeus subsequent to 1738 obscured the circumscription of *P. epiphyllanthus* by including under it as synonyms several other distinct species of sect. *Xylophylla*. As we shall see, this excessive liberality in ascribing synonyms also led to difficulty with Linnaeus's other species of *Phyllanthus*. In the "Hortus Cliffortianus" only one of the eight synonyms cited, that of Sloane, represents a different element from *P. epiphyllanthus*; but when Linnaeus acquired Patrick Browne's Jamaican collections, he incorrectly incorporated both of Browne's species into his herbarium as *P. epiphyllanthus*. Since neither of these specimens had been seen by Linnaeus during the writing of the "Species Plantarum," the specimen in the "Hortus Cliffortianus" Herbarium must be regarded as the type.

Browne's erroneous description (Civ. Nat. Hist. Jam. 188. 1756) of his *Phyllanthus 1* was the cause of additional confusion, for he mistook the disk-segments of the female flower for anthers. Linnaeus, thus misled into thinking that the flowers of the Jamaican plant were hermaphrodite, established (Mant. 147. 1771) the new genus *Xylophylla* with its type species *X. latifolia* L. However, the specific name is superfluous and hence illegitimate, because Linnaeus cited *P. epiphyllanthus* as a synonym of it. It is clear from this and from Linnaeus's annotation of both of Browne's specimens that he considered all the American representatives of *Xylophylla* † to belong to a single species.

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letter to Haller of 3 January 1738 states: "Though the *Hortus Cliffortianus* has long been printed, it is not yet published, owing to the tardiness of the engravers." In his letter to Haller of March, 1738 (op. cit. 322), Linnaeus observes: "Mr. Cliffort does not intend writing till he can send you his *Hortus*, which I hope he will be able to do in a fortnight, or three weeks at longest."

* The Paradisi Batavi Prodromus follows the Schola Botanica (ed. Simon Warton) in the same volume which is paged continuously: Schola pp. 1–300, Paradisi pp. 301–386.

† Linnaeus included one other species, *Xylophylla longifolia,* based on the Moluccan *Xylophyllos ceramica* of Rumphius (Herb. Amb. 7: 19–20, *pl. 12*. 1755). Although it proved to be a species of *Exocarpus* (Santalaceae), this was the element from which Linnaeus adopted his generic name.

Swartz at first (Prodr. 28. 1788) accepted *Xylophylla* as a distinct genus, and due to Linnaeus's confused interpretation in the "Mantissa" was led to redescribe *P. epiphyllanthus* as a "new" species, *Xylophylla falcata* Sw. Later (Observ. Bot. 113. 1791) he recognized the confusion, and realigned the species with comparative success. He restricted the references of Commelin and Catesby to *X. falcata*, and those of Plukenet (Phytogr. *pl. 247, fig. 4.* 1692; Almagest. Bot. 154. 1696), Sloane (Nat. Hist. Jam. 80. 1707), and Browne to *Xylophylla latifolia.* Although he incorrectly referred some references to *X. angustifolia* Sw., this fortunately made no difference as far as later nomenclature is concerned. Swartz's revision, by removing all the extraneous elements, effectively typified *Xylophylla latifolia.* When he later (Flor. Ind. Occ. 1109. 1800) reduced *Xylophylla* to a synonym of *Phyllanthus* and transferred the species in question, the epithet *latifolia* was at last legitimized (according to present rules) in the combination *Phyllanthus latifolius* Sw.

As Fawcett and Rendle (Jour. Bot. **57**: 67. 1919) have pointed out, the typical element of *P. latifolius* Sw. must be the *Phyllanthus 1* of Browne; the holotype is therefore the Browne specimen in the Linnaean Herbarium. This species is characterized by female flowers with the disk divided into discrete segments, which were mistaken by both Browne and Swartz for stamens. However, in Mueller's revision of the Euphorbiaceae (DC. Prodr. **15**[2]: 431. 1866), *P. latifolius* is described as having a cupuliform disk as high as the ovary; but Mueller's description was based on a specimen of Swartz in the Stockholm herbarium, not on Browne's collection. At this writing I have before me Swartz's specimens from the Riksmuseum, Stockholm; there are three sheets labelled *Phyllanthus* (or *Xylophylla*) *latifolia*, but only one label is written in Swartz's hand. The other two specimens are in the hand of Wikstroem, and it is these which represent the different species interpreted by Mueller as *P. latifolius.* It seems evident that Mueller was misled by some confusion in labelling in the Swartzian herbarium, and that Fawcett and Rendle were correct in considering Mueller's plant as an undescribed species, which they named *P. swartzii* Fawc. & Rend. Unfortunately, they overlooked the previously published *P. swarzii* Kostel. (Allgem. Med. Pharm. Fl. 1771. 1836), based on an entirely different species in sect. *Phyllanthus* which was also collected in Jamaica by Swartz.

The plant confused by Mueller and renamed by Fawcett and Rendle represents a population confined to the hills of western Jamaica, between Dolphin Head and the Cockpit Country, but perhaps extending to near the coast.* Its incrassate floral receptacles, urceolate female disk, and stylar column as high as the ovary make it a morphologically very distinct entity. In many respects, indeed, it approaches *P. coxianus* Fawc. & Rend., from St. Ann and Trelawney parishes, which has brilliant red flowers of similar aspect and is vegetatively very similar as well. But on the basis

* In addition to the two sheets in the Riksmuseum there is also a specimen in Herb. Mus. Brit. labelled "Jamaica. Seacoast. Dr. Swartz." Evidently Swartz confounded this plant with true *P. latifolius* on the basis of its close vegetative resemblance.

of our present knowledge, the morphological discontinuity being so profound, the population in question seems best designated in the rank of species. Because of the preoccupation of name mentioned above, it is here designated as **Phyllanthus dingleri** (nom. nov.: *P. swartzii* Fawc. & Rend. Jour. Bot. **57**: 67. 1919; non *P. swarzii* Kostel., 1836), in honor of Hermann Dingler (1846–1937), whose exhaustive researches on the morphology of sect. *Xylophylla* are eminently deserving of recognition.

With this perhaps over-lengthy discussion we have covered the history of *P. epiphyllanthus* L. and its literary offspring. One more point must still be mentioned. As noted above, the name *Phyllanthus* was first applied in 1689 by Hermann (as *Phyllanthos*) to *P. epiphyllanthus*, doubtless because the floriferous phylloclades appeared to be leaves with flowers in marginal notches. It might be supposed, therefore, that *P. epiphyllanthus* would be the type of the genus. This is a matter of some importance, because the phylloclade-bearing species have even in recent times occasionally been considered as constituting a distinct genus *Xylophylla* (e.g., L. H. Bailey, New Man. Cult. Plants). *Xylophylla latifolia* L. has already been shown to be based on the same type as *P. epiphyllanthus* L., so that if the latter species is considered the type of *Phyllanthus*, *Xylophylla* must be rejected as a superfluous and illegitimate name.

Hitchcock and Greene, in their compilation of "Species Lectotypicae Generum Linnaei" (Brittonia **6**: 114. 1947) selected *Phyllanthus niruri* L. as the type of the genus. While their decision was likely purely arbitrary, it is supported by a critical study of Linnaean literature. In the first edition of the "Genera Plantarum" (1737, p. 282) Linnaeus noted that the floral characters were provided by *Niruri* (= *P. niruri* L.), although the name of the genus was taken from *P. epiphyllanthus*. Since for Linnaeus, floral characters always took precedence over vegetative ones in the definition of genera, it would seem only logical to fix on *P. niruri* as the type. His removal of *P. epiphyllanthus* to a separate genus *Xylophylla* even more obviously points to the same conclusion.

The matter, however, is not settled with the choice of *P. niruri* L. as the generic type. This species, as it happens, has been consistently misinterpreted by subsequent authors, the "Phyllanthus niruri" of recent floras and manuals almost invariably being one or more species different from the plant described by Linnaeus. The confusion is perhaps best documented in the treatment given the name by Mueller Argoviensis (DC. Prodr. **15**[2]: 406. 1866). Here *P. niruri* is interpreted as composed of six varieties; actually, these entities represent five distinct species, no one of which is the *P. niruri* of Linnaeus!

Mueller (loc. cit.) noted under *P. niruri β genuinus* that he had seen an authentic specimen in the Linnaean Herbarium, but the specimen annotated "Niruri" in the Linnaean Herbarium (sheet 1105–2) obviously represents a different species from *P. niruri* sensu Mueller. The narrow, almost acicular, stipules of the plant are quite unlike the broader lanceolate ones of the plant mistaken for *P. niruri* by Mueller. The specimens in the Hortus Cliffortianus and Hortus Upsaliensis Herbaria are obviously con-

specific and even have the appearance of duplicates that were collected at the same time. When this is taken into account together with Linnaeus's description of the position of the sexes (Hort. Upsal. 282. 1748), there can be little doubt as to the plant described by Linnaeus as *Phyllanthus niruri*; it is the West Indian form of the widespread New World species currently passing as *P. lathyroides* H.B.K.

Research into the original citations given by Linnaeus in the "Hortus Cliffortianus" has made it possible to unravel some of the mystery surrounding the species. The specific epithet *niruri* was based, as was Linnaeus's wont, on a generic name: *Niruri*. First published by Rheede tot Draakestein (Hort. Malabar. 2: 45, *fig. 27*. 1679 [misquoted by Linnaeus as vol. 10, *fig. 27*]), it was adopted by Martyn (Hist. Pl. Rar. *pl. 8*. 1728) as the generic name for a West Indian species. Martyn's plant, splendidly illustrated in the first color-printed botanical book, bore the name *Niruri barbadense . . . petiolis florum brevissimis*. This name actually was originated by Isaac Rand in a list of plants presented to the Royal Society from the Chelsea Gardens by the Company of Apothecaries (Trans. Roy. Acad. 35: 293–296. 1727). Linnaeus's use of the epithet *niruri* and his assignment of the species to Barbados (with only a questionable reference to Malabar) plainly indicates that in the "Hortus Cliffortianus" he was describing the plant of Martyn and of Rand. In the preface of that work he acknowledges the receipt of tropical American plants from Philip Miller, and he may have obtained *P. niruri* in 1736 when he visited Miller at the Chelsea Gardens.*

The confusion which has attended the name *P. niruri* to the present day is due in large part to Linnaeus's inclusion under it of synonyms which actually belong to different species. His remark following the listing of the species in the "Hortus Cliffortianus" explains his attitude: "Variat foliorum figura & magnitudine, hinc plure tenentur species quam re ipsa sunt." Linnaeus would in this instance have done well to heed the advice of Haller (letter of 17 Oct. 1748, transl. Smith, Select. Corr. Linnaeus 2: 431. 1821): "Do not strike out species, and reduce them to varieties, so frequently as you are accustomed . . . I cannot, without concern, see good and genuine plants perish, as it were, and become lost to botanists, under the title of varieties."

Haller's warning was prophetic as far as concerns *P. niruri*, for the overly broad concept adopted by Linnaeus has led subsequent botanists to place at least a dozen different herbaceous species of *Phyllanthus* under this one name. Linnaeus's indication of range in the "Species Plantarum" of 1753 as merely "in Indiis" certainly encouraged these later misidentifications. In fairness to Linnaeus, however, it should be made clear that not

* Rand's comment on the plate of *P. niruri* in his review of Martyn's "Historia Plantarum Rariorum" (Trans. Roy. Acad. 36: 5. 1729) would indicate that Martyn's plant was the one from the Chelsea Gardens. Furthermore, Rand's specimen and a duplicate sheet with the notation "Herbar Miller" are preserved in Herb. Mus. Brit. Evidently, therefore, Martyn, Rand, Miller, and Linnaeus all were dealing with duplicates or descendants of the same stock in the Chelsea Gardens.

only are some of the relatives of *P. niruri* "cryptic" species which are superficially very similar, but also some of these weedy species appear to have very early been carried from one hemisphere to the other. Consequently, references in the "Species Plantarum" to illustrations of Plukenet, Rheede, et al., may be meaningless unless the specimens from which the illustrations were taken happen to be still in existence. For example, Linnaeus singled out the drawing by Plukenet (Phytogr. *pl. 183, fig. 5*) as "good" for *P. niruri*; but an examination of Plukenet's specimens * shows that the plant is poorly depicted in the drawing and certainly is not the species which Linnaeus had before him when writing the account in the "Hortus Cliffortianus."

The treatment of *P. niruri* by Mueller must now be gone into more thoroughly, since his work has been followed by the majority of later workers. I have already pointed out that the plant designated by Mueller as *P. niruri β genuinus* is not the same species as *P. niruri* L.; the latter differs from Mueller's plant by its much narrower and longer stipules, unisexual cymules, and verruculose rather than striate seeds. Yet Mueller claimed (DC. Prodr. 15|2|: 406. 1866) to have seen an authentic specimen in the Linnaean Herbarium. The sheet which is obviously true *P. niruri* (1105–2) was annotated as such by Linnaeus; but there is one specimen among the Linnaean collection which represents *P. niruri* sensu Mueller. It is on the right-hand side of sheet 1105–5; but the left-hand specimen is *P. urinaria* L. and the sheet is pinned to sheet 1105–4, which is also *P. urinaria*, and annotated as such by Linnaeus. It seems probable, therefore, that the plant which Mueller equated with *P. niruri* was considered by Linnaeus to be only a form of *P. urinaria*. It is consequently difficult to understand why Mueller ignored sheet 1105–2, plainly marked as *Niruri*.

The result of Mueller's misinterpretation has been a curious duplex adaptation of the name *P. niruri*. The plant originally introduced into the Chelsea Gardens and given to Linnaeus by Miller appears to have been distributed to several different botanical gardens under the correct name. Thus when Pax illustrated *P. niruri* from a living plant in the first edition of the "Natürlichen Pflanzenfamilien" (3[5]: *fig. 14*. 1890), the plant was correctly identified; but the vast majority of the dried specimens in the Berlin herbarium under that name were doubtless misidentified, as they were everywhere else. Most of these mislabelled specimens represent a single weedy species, which has become circumtropical, in contrast to the strictly American *P. niruri*.

We now have to determine the correct name of this usurper which Mueller designated as *P. niruri β genuinus*. The first post-Linnaean author

* There are in Plukenet's Herbarium, which is incorporated in Herb. Sloane at Herb. Mus. Brit., two collections associated with plate 183, fig. 5 of the "Phytographia." The first, vol. 92 p. 173, which bears the legend "ex Coromandel," is of special interest in indicating that this West Indian species, *P. amarus* Schum. & Thon., had reached India before 1690. The second, vol. 96 p. 46, is also *P. amarus*; Plukenet appears not to have had true *P. niruri* L.

to deal critically with the identity of *P. niruri* was F. K. Medicus, who in his monograph of the Malvaceous Alliance (1787) published the name *Urinaria erecta*, apparently based on John Burman's *Urinaria indica, erecta, vulgaris* (Thes. Zeyl. 230. 1737). The identity of Burman's plant is uncertain,* but in any event *Urinaria erecta* Medic. is not Mueller's plant, as is evident from Medicus's earlier description (Bot. Beobacht. 263. 1783) of the inflorescence and flowers. In fact, in the earlier reference Medicus called his plant *P. niruri*, and — judging from his description — correctly so. Since Medicus proposed *Urinaria erecta* as a deliberate substitution for *P. niruri* L. (he said he was "restoring the older name,") his name is not only synonymous but also superfluous and hence illegitimate.

Recently, when dealing with the herbaceous species of sect. *Phyllanthus* for the West Indies (Contr. Gray Herb. 176: 53. 1955), I thought that the two species confused under the epithet *niruri* had been first distinguished by Kosteletzsky (Allg. Med. Pharm. Fl. 1771. 1836). Following his description of *P. niruri*, to which are correctly ascribed male flowers "unten und gepaart" and female "oben und einzeln," he added:

"In Jamaika findet sich eine sehr ahnliche Art: *Ph. Swarzii*. (Ph. Niruri. Sw.) welche jedoch nur einzelne Blüthen in den Blattachseln (die ♂ und ♀ gemengt unter einander) und 5-theilige Kelche besitzt."

The new species was presumably based on Swartz's description of "Phyllanthus niruri" in his "Observationes Botanicae," pp. 354–355 (1791); there is no way of being sure if Kosteletzsky saw a specimen of Swartz. In Swartz's herbarium in the Riksmuseum, Stockholm, there are a number of sheets annotated by him or by some of his colleagues as *P. niruri*. No less than three species are represented, but only one of these has the flowers arranged in the manner which fits the descriptions of Swartz and Kosteletzsky. This species is the one designated by Mueller as *P. niruri β genuinus*, and I therefore (loc. cit.) adopted *P. swarzii* Kostel. as the correct name for the plant.

However, since then and while studying the collections in Herb. Kew, I have discovered that Kosteletzsky's proposed species had been anticipated by the *P. amarus* of Schumacher and Thonning (Beskr. Pl. Guin. 2: 195–196. 1829), based on a type from West Africa which I had not examined. I had partially been misled by the fact that Mueller (DC. Prodr. 15[2]: 407. 1866) associated *P. amarus* with *P. debilis* Willd., a very different species. However, drawings and observations of the type specimen (in Herb. Copenhagen) made by Brenan and deposited in Herb. Kew, together with his excellent published discussion (Kew Bull. 1950: 215–218. 1950),

* Burman's second species, *Urinaria zeylanica repens cauliculis rubentibus* (op. cit. 231) is represented in Herb. Hermann (BM) by three specimens on the following sheets: vol. 2, p. 7; vol. 3, p. 55; vol. 4, p. 41. These, and illustrations nos. 11 and 429 of Hermann's "Icones" (also in Herb. Mus. Brit.), certainly represent *P. urinaria* L. But there appear to be no specimens of *Urinaria indica, erecta, vulgaris*; and of the two Icones supposed to refer to this species, no. 53 appears to be a *Breynia*, while no. 56 suggests the widespread weedy species of sect. *Menarda*, *P. tenellus* Roxb. The illustration in the "Thesaurus" represents a different herbaceous species which could be *P. amarus* but whose exact identity must remain in doubt.

leave no doubt as to the identity of the species in question. Brenan's description of the unisexual cymules — which Schumacher and Thonning, like Kosteletzsky, recognized as a chief distinguishing character of the species — clearly indicates that *P. niruri β genuinus* Muell. Arg. and *P. swarzii* Kostel. are synonyms of *P. amarus* Schum. & Thon. It is to this last species that many, perhaps most, of the Old-World records of "Phyllanthus niruri" must be referred.

As previously mentioned, the true *P. niruri* L. is native of and restricted to the New World. There is every reason to believe that *P. amarus* is also natively an American species, although it (as "Phyllanthus niruri") has in many floras been indicated as native to the Old World. The closest relative of *P. amarus*, however, is certainly *P. abnormis* Baill., a plant confined to sandy areas in Texas and Florida which has the same flower-arrangement and differs only in its perennial habit and larger fruit. It is therefore most likely that *P. amarus* originated in the Caribbean area as a vicarious species of *P. abnormis* of the southern U. S., but was in early colonial days spread around the tropics by trading vessels.

On the other hand, as is the case with several other American species, *P. amarus* shows a rather close relationship to one Old World species.* This plant, which was designated by Mueller (Linnaea 32: 43. 1863) as *P. niruri β scabrellus*, is superficially so like *P. amarus* that the two have almost invariably been confused. In my recent consideration of the West Indian species (Contr. Gray Herb. 176: 53. 1955), I applied the new specific name *P. fraternus* to this plant, which appears to be originally native to Pakistan and India but which has appeared in a few widely-scattered localities in the West Indies. However, while making a routine survey of the collections in Herb. Kew, I discovered that Hutchinson had already in 1920 independently described this species from a South African collection as *P. asperulatus* Hutch.; this well demonstrates how difficult it is, despite the greatest precautions, to establish and define specific names in this complex of widely and capriciously distributed weeds.

In order to finish this detective story of what happened to *P. niruri*, we now have to return to *P. niruri* sensu Swartz (Obs. Bot.). Swartz's description has been shown to have served as the basis for *P. swarzii* Kostel., but this disposes of only one of the three elements included therein. The erratic C. S. Rafinesque now enters upon the stage, for he also based a new species on *P. niruri* sensu Sw. in his "revision" of *Phyllanthus* (Sylva Tellur. 91–92. 1838). In Rafinesque's own words, his attempt "must be deemed very imperfect"; one can surmise from such uncharacteristic modesty that this is an understatement. The "revision," in fact, reveals a shocking lack of taste and judgment even for Rafinesque, and one can understand why it was ignored *in toto* by Mueller.

Nevertheless, there is one passable specific description in the article,

* As examples may be adduced the evident close relationships of *P. niruri* and *P. stipulatus* with *P. benguelensis* and *P. microphyllinus*, respectively, both the latter from west Africa.

under the genus *Moeroris* (taken from Rumphius's name for some herbaceous species of *Phyllanthus*):

"MOERORIS Raf. diff. cal. 5phyl. glandulis 5 ad basis, caps. 3loc. 6valv. . . *Moeroris stipulata* Raf. Phyll. niruri, Swartz. Herbacea, foliolis obl. glaucis subsess. stipulis 2 geminatis coloratis, fl. axil. ped. nutantib. — Mts. of Jamaica."

As with Kosteletzsky's description, so this too appears to be taken from the treatment in the "Observationes Botanicae." But the details specified by Rafinesque — "stipulatis 2 geminatis coloratis" and "Mts. of Jamaica" — effectively eliminate two of the three elements in the Swartzian concept. Kosteletzsky's plant, (*P. amarus*) is rather unusual among the West Indian herbaceous species in having stipules which are *not* at all reddish-tinged; and the third element, which according to Swartz (loc. cit.) was collected on Hispaniola, proves to be *P. fuertesii* Urb., a species which does not occur in Jamaica. This leaves as representing Rafinesque's name the plant with reddish stipules and the flower arrangement (though not the seeds) of *P. niruri* L. It is the widespread species of swampy habitats in tropical America which at present goes under the name of *P. diffusus* Kl. This species must now be known as *P. stipulatus* (Raf.) Webster (Contr. Gray Herb. **176**: 53. 1955).

No doubt it may appear unusual and even undesirable that two different species should both be based on *P. niruri* sensu Sw., but the application of modern principles of typification leads irresistibly to this conclusion. In a sense, the species of both Kosteletzsky and Rafinesque may be said to have been established by "blind luck," for it is quite possible that both authors merely pilfered from Swartz's description without seeing any specimens. But in evaluating their proposed names we must give these authors the benefit of the doubt, particularly since their names can be associated with definite specimens.

The history of the first two species described in the "Hortus Cliffortianus" having been followed out to what may appear painful lengths, we have to consider the third species, *P. grandifolius* L., which has been as badly misinterpreted as *P. niruri*. Linnaeus's original description (Hort. Cliffort. 439) is brief:

3. PHYLLANTHUS caule arboreo, foliis ovatis obtusis integerrimis. Niruri arborescens, foliis singularibus subrotundis & subtus incanis, fructo maximo. *Houst. mss. Crescit in* America, *communicata per Millerum. Folia magnitudine palmi, subtus glauca.*

Even from this short description, it is easy to guess what species is indicated, and this is confirmed by examination of the specimen in the Hortus Cliffortianus Herbarium. It consists of a sterile branch mounted with Houston's manuscript label, and is obviously the species which was described in 1817 from a Campeche collection as *P. glaucescens* H.B.K.

Some generally overlooked additional information about *P. grandifolius* is furnished by Philip Miller (Gard. Dict. ed. 8. 1768), who redescribed the same plant,* apparently having overlooked Linnaeus's account:

* There is in Herb. Mus. Brit. a sheet of *P. grandifolius* with the MS label: "Niruri

3. ANDRACHNE (*Arborea*) foliis ovatis obtusis, subtus incanis, caule arboreo. . . discovered by the late Dr. William Houston, growing naturally at Campeachy. . .

This clears up the mystery of *Andrachne arborea* Mill., a name which Mueller overlooked and which Pax and Hoffmann (Pflanzenr. IV. 147. XV.: 178. 1922) were unable to place, remarking it as "vix recognoscenda et omnino dubia."

Mueller Argoviensis unfortunately brought the application of *P. grandifolius* into serious confusion by applying the name to an entirely different plant from the West Indies, which does not occur in Mexico or Central America. This West Indian plant had been described by Willdenow (Enum. Pl. Hort. Berol. Suppl. 64. 1813) as *P. juglandifolius*. Willdenow gave as a synonym "Phyllanthus grandifolius *Hortul.*," indicating that the plant had acquired this name while in cultivation. Herbarium sheets of the species collected from various European botanic gardens in the early nineteenth century often bear this name, which was simply a misidentification.

Since Willdenow's name was accepted for the West Indian plant by Grisebach (Pl. Wright. 1: 158. 1860) and Baillon (Adansonia 1: 38 39. 1860 61) not long before Mueller's revision, it is difficult to see what led to the latter's erroneous application. Even if Mueller did not look at the original description in the "Hortus Cliffortianus," an attentive reading of the passage in the "Species Plantarum" should have sufficed to show that Linnaeus was not dealing with the West Indian plant. The phrase "foliis ovatis obtusis integerrimis" clearly sets the plant off from the other five species included in *Phyllanthus*, all of which (except possibly *P. maderaspatensis*) Linnaeus considered to have either pinnate or crenate leaves. As is suggested by Willdenow's choice of the epithet *juglandifolius*, the West Indian plant would certainly have been considered pinnate-leaved by Linnaeus.

There can be no doubt, therefore, that *P. juglandifolius* Willd. is the name which must be applied to the West Indian species called *P. grandifolius* γ *genuinus* by Mueller. The plant interpreted by Mueller as *P. glaucescens* H.B.K. must be called *P. grandifolius* L. Although a number of species closely related to *P. glaucescens* have been described, it is highly probable that that species is a positive synonym of *P. grandifolius* L., for both were collected from the same region, and the type specimen in the Hortus Cliffortianus Herbarium closely resembles typical material of *P. glaucescens*.

The impression which remains from this excursion into the Augean stables of nomenclature is that the typification of Linnaean species was not considered very seriously by Mueller, or most of the authors succeeding him. The interpretations adopted here are those which fix the Linnaean

fructo maximo Houst. ms. 159. Campeachy, Houston." This sheet, presumably from Herb Miller, is evidently a duplicate of that in the Hortus Cliffortianus Herbarium, so that Miller's and Linnaeus's species are exact synonyms.

names to the plants actually familiar to Linnaeus himself. It must be admitted, of course, that this is possible chiefly because authentic specimens are available in the various Linnaean herbaria; it would have been impossible, in the instance of *P. niruri*, ever to have untangled the confusion on the basis of the illustrations cited by Linnaeus and later authors.

Svenson (Rhodora **47**: 388. 1945) has pointed out that the Linnaean species is an aggregate — often of several different species by modern standards — based on descriptions, plates, dried specimens, and living plants. He concludes that since "all synonyms seem to have been of equal value . . . selection of a representative element for each species would seem largely dependent on usage." The involved discussions in the present paper certainly illustrate how much caution should be exercised in selecting "representative elements," but I cannot agree that "usage" is the touchstone to solve the problem. In fact, the dangers attendant on typifying species through "usage" are very great; it was exactly by such an adoption of usage that Mueller made such serious errors in interpreting two of Linnaeus's three American species of *Phyllanthus*. When, as in the nomenclatural history of *P. niruri*, usage is so ill-informed and remote from biological reality, it is futile to expect that it can provide any stability. The only positive course to follow in interpreting Linnaean species is to determine which of the elements of the species were personally familiar to that author and, wherever possible, to designate a particular specimen as holotype. Even though this may not always be possible, taxonomists should attempt to reduce the chaos as much as possible.

SUMMARY

Linnaeus in the "Hortus Cliffortianus" described three American species of *Phyllanthus* which in the "Species Plantarum" became *P. epiphyllanthus*, *P. niruri*, and *P. grandifolius*. Material of the latter two species was probably given to Linnaeus by Philip Miller, of the Chelsea Gardens; and Linnaeus was familiar with *P. niruri*, at least, from living specimens. Linnaeus took the generic name from Hermann's original citation of *P. epiphyllanthus*, but based the generic character on the flower of *P. niruri*. The latter species is therefore the generic type.

Linnaeus confused the application of *P. epiphyllanthus* by erroneously including with it some distinct species collected in Jamaica by Patrick Browne, and redescribed the entire ensemble as a new genus and species *Xylophylla latifolia*, because of a misinterpretation of Browne's floral description. Olaf Swartz, though still misinterpreting the flower structure, nevertheless reduced *Xylophylla* to the synonymy of *Phyllanthus* and redefined *P. epiphyllanthus* and *P. latifolius*. The latter species was misconstrued by Mueller Argoviensis, who confounded it with an undescribed species of Swartz finally established as *P. swartzii* Fawc. & Rend.; the latter name being preoccupied, *P. dingleri* Webster is proposed in its stead.

Linnaeus's *P. niruri*, though well defined in the "Hortus Cliffortianus," became confused owing to his erroneous conclusion of other species as

synonyms, and to later misidentifications by subsequent authors. The commonest weedy species so mistaken for *P. niruri*, by Mueller and others, was defined as *P. swarzii* by Kosteletzsky in 1836, based on the *P. niruri* of Swartz; but the earliest name for it appears to be *P. amarus* Schum. & Thon., as established by Brenan. Another weedy species also often confounded with *P. niruri*, was — by a curious coincidence — also based on Swartz's *P. niruri* by Rafinesque. Rafinesque's epithet having priority over the generally accepted *P. diffusus* Kl., the species in question must be known as *P. stipulatus* (Raf.) Webster.

Linnaeus's *P. grandifolius*, based on a collection of William Houston from Campeche, became confused owing to the name being misapplied to a very different West Indian species. The latter, *P. juglandifolius* Willd., was correctly interpreted until the monograph of Mueller Argoviensis, who adopted the prevalent horticultural misidentification and called Willdenow's plant *P. grandifolius*. The latter name must now be adopted for the plant currently passing as *P. glaucescens* H.B.K., and Willdenow's name readopted.

It is concluded that Svenson's appeal to "usage" as the determining factor in typifying Linnaean species is futile, and that the only practicable course is to fix the names on actual specimens, if at all possible.

NOMENCLATURAL RESUME *

Phyllanthus epiphyllanthus L. Sp. Pl. 981. 1753.

Phyllanthos americana planta, flores e singulis foliorum crenis proferens Herm. Par. Bat. Prodr. 365. 1689; Commelin, Hort. Med. Amst. Rar. Pl. 199–200. *fig. 102.* 1697; Catesb. Nat. Hist. Carol. 26, *pl. 26.* 1725 [*Catesby* (BM)].

Phyllanthos Americana angustiora & longiori ramosa &c. Pluk. Phytogr. 3: *pl. 247, fig. 4.* 1692 [Herb. Sloane 97: 100; 101: 106 (BM)].

Phyllanthus foliis lanceolatis serratis: crenis floriferis L. Hort. Cliffort. 439. 1738 (excl. ref. Sloane & Plukenet) [Herb. Hort. Cliffort. (BM)].

Xylophylla latifolia L. Mant. Alt. 221. 1771 (ex. p., excl. ref. Browne); non *X. latifolia* Sw.

Xylophylla falcata Sw. Prodr. 28. 1788 [*Swartz* (S, HOLOTYPE)].

Phyllanthus falcatus Sw. Fl. Ind. Occ. 2: 1115. 1800.

Xylophylla epiphyllanthus (L.) Britton in Small, Fl. Florida Keys 76. 1913.

Exocarpus epiphyllanthus (L.) Merr. Interpr. Rumph. Herb. Amb. 208. 1917.

Phyllanthus latifolius Sw. Fl. Ind. Occ. 2: 1109. 1800.

Hemionitidi affinis Americana epiphyllanthos &c. Pluk. Phytogr. 1: *pl. 36, fig. 7.* 1691 [Herb. Sloane 90: 51 (BM)].

* The references in brackets indicate the herbarium material examined by me on which the descriptions, and often the illustrations, are based. The numbers of Herb. Sloane refer to the volume and page numbers of this large herbarium, which is bound in folios and kept in separate cabinets in Herb. Mus. Brit. The abbreviations otherwise are the standard ones of Lanjouw and Stafleu. The synonymy does not purport to be complete; only the older names or those specially relevant are cited.

Lonchitidi affinis arbor anomala folio &c. Sloane, Cat. Pl. Jam. 16. 1696; Nat. Hist. Jam. 1: 80. 1707 [Herb. Sloane 1: 62 (BM)].

Phyllanthus 1. Foliis latioribus utrinque acuminatis &c. Browne, Civ. Nat. Hist. Jam. 188. 1756 [Herb. Linn. 1105–1 (LINN)].

Xylophylla latifolia L. Mant. Alt. 221. 1771 (as to the plant of Browne only); Sw. Prodr. 28. 1788; Obs. Bot. 113. 1791.

Phyllanthus isolepis Urb. Symb. Ant. 3: 290. 1902 [Ferry Pen, Jamaica, *Campbell 6280* (NY, fragment of type)].

Phyllanthus dingleri Webster, nom. nov. [Jamaica, *Swartz* (S, HOLOTYPE; BM, ISOTYPE)].

Phyllanthus latifolius sensu Muell. Arg. in DC. Prodr. **15**(2): 431. 1866; non Linnaeus nec Sw.

Phyllanthus swartzii Fawc. & Rend. Jour. Bot. **57**: 67. 1919; non *P. swarzii* Kostel., 1836.

Phyllanthus niruri L. Sp. Pl. 981. 1753 [Herb. Linn. 1105–2 (LINN)].

Niruri barbadense. . . petiolis florum brevissimis Rand, Trans. Roy. Soc. **35**: 295. 1727 [ex Chelsea Garden (BM)]; Martyn, Hist. Pl. Rar. *pl. 8.* 1728.

Phyllanthus foliis alternis alternatim pinnatis &c. L. Hort. Cliffort. 439. 1738 (excl. ref. Burm. & Rheede) [Herb. Hort. Cliffort. (BM, HOLOTYPE of *P. niruri*)].

Phyllanthus lathyroides H.B.K. Nov. Gen. & Sp. **2**: 110. 1817 [Herb. Humboldt (P, type collection)].

Phyllanthus purpurascens H.B.K. ibid. [Herb. Humboldt (P, type collecticn)].

Phyllanthus chlorophaeus Baill. Adansonia **1**: 27. 1860–61. [Mexico, *Jurgensen 858* (G, HOLOTYPE)].

Phyllanthus amarus Schum. & Th. Kongl. Danske Vidensk. Selsk. Skr. **4**: 195–196. 1829 * [type fragment ex Herb. Copenhagen & drawings of floral details by Brenan (K)].

Fructiculus capsularis, hexapetalis &c. Pluk. Phytogr. **3**: *pl. 183, fig. 5.* 1692 [Herb. Sloane 92: 173; 96: 46 (BM)].

Phyllanthus niruri sensu Sw. Obs. Bot. 354–355. 1791 (ex p.).

Phyllanthus swarzii Kostel. Allgem. Med. Pharm. Fl. 1771. 1836 [Jamaica, *Swartz* (S, HOLOTYPE)].

Phyllanthus niruri β genuinus Muell. Arg. in DC. Prodr. **15**(2): 406. 1866; et auct. seq., non *P. niruri* L.

Phyllanthus nanus Hook. f. Fl. Br. Ind. **5**: 298. 1887 [Burma, *Griffith* (K, HOLOTYPE)].

Phyllanthus stipulatus (Raf.) Webster, Contr. Gray Herb. 176: 53. 1955.

Phyllanthus niruri sensu Sw. Obs. Bot. 354–355. 1791 (ex p.).

Moeroris stipulata Raf. Sylva Tellur. 91–92. 1838 [Jamaica, *Swartz* (S, HOLOTYPE)].

* This is often cited as "Beskr. Guin. Pl.", a separately issued reprint usually considered as dating from 1827, but fide Fl. Males. (**4**: ccii. 1954) appearing in 1829.

Phyllanthus diffusus Klotzsch, Bot. Voy. Herald 105. 1853 [Panama, *Seemann 198* (K, HOLOTYPE)].

Phyllanthus asperulatus Hutch. Kew Bull. **1920**: 27–28. 1920 [Transvaal, *Schlechter 11866* (K, HOLOTYPE)].

Phyllanthus niruri β scabrellus Muell. Arg. Linnaea **32**: 43. 1863; not *P. scabrellus* Webb, as to type.

Phyllanthus fraternus Webster, Contr. Gray Herb. **176**: 53. 1955 [Punjab, *Thomas Thomson* (K, HOLOTYPE)].

Phyllanthus grandifolius L. Sp. Pl. 981. 1753 (as *P. grandifolia*).

Phyllanthus caule arboreo, foliis ovatis obtusis integerrimis L. Hort. Cliffort. 439. 1738 [Herb. Hort. Cliffort. (BM)].

Andrachne arborea Miller, Gard. Dict. ed. 8. 1768 ["Campeachy," *Houston* (ex herb. Miller, BM)].

Phyllanthus glaucescens H.B.K. Nov. Gen. & Sp. **2**: 115. 1817 [Campeche, Herb. Humboldt (P, type collection)].

Phyllanthus juglandifolius Willd. Enum. Pl. Hort. Berol. Suppl. 64–65. 1813 [Herb. Willdenow (B, HOLOTYPE)].

Phyllanthus grandifolius sensu Poir. Encycl. Method. **5**: 296. 1804; et auct. seq., non L.

Agyneia berterii Spr. Syst. Veg. **3**: 19. 1826 [Puerto Rico, *Bertero* (P)].

Phyllanthus quinquefidus Sessé & Moc. Fl. Mex. 212. 1894 [*Sessé et al.*, Pl. Nov. Hisp. (F, type collection)].

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A MONOGRAPH OF THE GENUS PHILADELPHUS *

SHIU-YING HU

With plates V and VI

Section 5. **Microphyllus** (Koehne), stat. nov.

Philadelphus subg. II. **Euphiladelphus** sect. 5. **Microphyllus** (Koehne), stat. nov.

Philadelphus Reihe 4. *Decorticatae pauciflorae* Koehne, Deutsche Dendr. 180, 184. 1893, pro parte.

Philadelphus sect. *Poecilostigma* subsect. *Microphylli* Koehne in Gartenfl. **45**: 450, 506. 1896; et in Deutsch. Dendr. Ges. **1904**(13): 78. 1904.

Philadelphus Microphylli Rydb. in N. Am. Fl. **22**: 163. 1905, in clavi, s. stat.

Philadelphus ser. *Microphylli* (Koehne) Rehder, Cult. Trees Shrubs ed. 2, 273. 1940; et Bibl. Cult. Trees Shrubs 194. 1949.

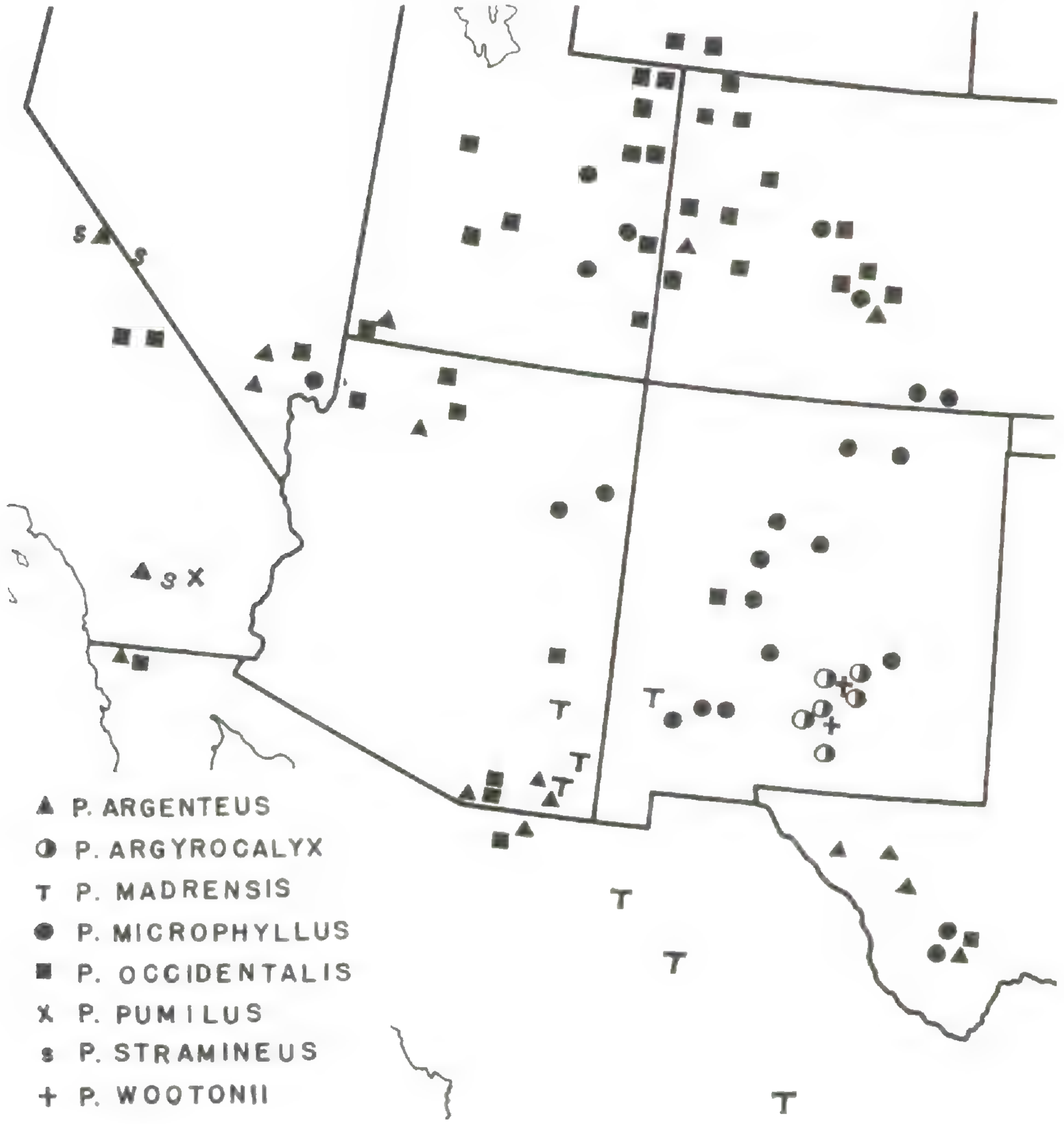
TYPE SPECIES: *P. microphyllus* Gray.

Compact low shrubs less than 2 m. high, the bark exfoliate, rarely closed; leaves small, ovate, rarely elliptic or lanceolate, usually less than 2 cm. long, entire and ciliate, generally densely pubescent beneath; flowers solitary, rarely ternate; hypanthium pubescent, usually incanous or lanate; petals white, sometimes purple at the base; stamens 35–50, rarely less than 25; disc and style generally glabrous; capsules subglobose, rarely ellipsoid or turbinate; seeds usually very short caudate.

Species in this section are xerophytic. In order to adapt themselves to an arid condition of living, in the course of evolution different species have acquired different types of indumentum on their small leaves and flowers. These hairs can be employed as a convenient means for the identification of species.

Species of this section are concentrated in the semidesert area of the southern Rocky Mountains, extending southward to northern Mexico. As shown in Map 6, most of the species are isolated endemics. *Philadelphus occidentalis* and *P. microphyllus* are two relatively widespread species. Their ranges overlap in central and western Colorado, eastern Utah, Clark County in Nevada, and Brewster County in Texas. Nevertheless there is a difference in the general area of their concentration. *Philadelphus occidentalis* occurs in the north and west, while *P. microphyllus* is confined to the southeast. The area of *P. argenteus* is rather wide, but its degree of concentration is low. The distribution of the species of this section is shown in map 7.

* *Continued from volume XXXVI, page 368.*



MAP 7. The distribution of the species of *Philadelphus* in the section Microphyllus.

KEY TO THE SPECIES

A. Hypanthium and sepals glabrous or only sparsely pilose at the base. . . . . 50. *P. microphyllus.*

AA. Hypanthium and sepals uniformly pubescent.

B. Leaves glabrescent or sparsely villose above; hypanthium lanate.

C. Corolla cruciform; base of the style glabrous; seeds long-caudate; upper surface of the leaf glabrous. . . . . 51. *P. argyrocalyx.*

CC. Corolla disciform; base of the style pubescent; seeds short-caudate; upper surface of the leaves sparsely villose. . . . . 52. *P. wootonii.*

BB. Leaves strigose or hispid above; hypanthium incanous or slightly pilose, the hairs straight and appressed.

C. Pubescence on both surfaces of the leaves appressed.

D. Hypanthium slightly pilose, the epidermal tissue visible. . . . . 53. *P. occidentalis.*

DD. Hypanthium thickly covered, the hairs incanous, the epidermal tissue obscured, the indumentum consisting of straight strigose hairs mixed with some weak crisp ones.
E. Leaves ovate-oblong; corolla disciform. . . 54. *P. argenteus*.
EE. Leaves lanceolate or ovate-lanceolate; corolla subcampanulate.
F. Flowers white; base of the style glabrous; leaves canescent beneath. . . . . 55. *P. palmeri*.
FF. Flowers purple-centered; base of the style hirsute; leaves sparsely pilose beneath. . . . . 56. *P. maculatus*.
CC. Pubescence on the upper surface erect, hispid, mixed with some villose appressed hairs.
D. Filaments of the stamens distinct; pubescence on the hypanthium and the lower leaf surface appressed.
E. Leaves 10–18 mm. long, 5–8 mm. wide; corolla disciform; disc pubescent. . . . . 57. *P. stramineus*.
EE. Leaves 5–10 mm. long, 2–4 mm. wide; corolla cruciform; styles and disc glabrous. . . . . 58. *P. pumilus*.
DD. Filaments of 3 or 4 stamens united; pubescence on the lower leaf surface dense, long-villose, more or less erect and spreading. . . . . 59. *P. madrensis*.
BBB. Leaves pilose or villose above, the hairs appressed; densely long-villose beneath, the hairs erect; hypanthium incanous, the hairs long-villose, straight or slightly curly. . . . . 60. *P. crinitus*.

50. **Philadelphus microphyllus** Gray in Mem. Am. Acad. Sci. II. **4**: 54. 1849. — Walpers, Ann. **2**: 614. 1851. — Port. & Coult., Synop. Fl. Colorado 41. 1874. — Anon. in Wien. Ill. Gart.-Zeit. **12**: 435, *fig. 86*. 1887. — Nicholson in Gard. Chron. III. **2**: 156, *fig. 36*. 1887. — Goldring in Garden **34**: 134, [*fig. 1*]. 1888. — T[hompson] in Garden **40**: 289, [*pl. 1*]. 1891. — Anon. in Gard. Chron. III. **11**: 86, *fig. 17*. 1892; et **51**: 225, *fig. 101*. 1912. — Dippel, Handb. Laubh. **3**: 340. 1893. — Koehne, Deutsche Dendr. 184. 1893; in Gartenfl. **45**: 506. 1896; et in Mitt. Deutsch. Dendr. Ges. **1904**(13): 78. 1904. — Schneider, Ill. Handb. Laubh. **1**: 365, *fig. 234, e — f*[2]. 1905. — Rydb. in N. Am. Fl. **22**: 172. 1905. — [Weathers] in Gard. Album **1**: 68, *pl. 17*. 1906. — Standley in Contr. U.S. Nat. Herb. **13**: 190. 1910. — Clements, Rocky Mt. Fl. Pl. 31. 1914. — Armstrong, Field Book West. Wild Fl. 209. 1915. — Wooton & Standley in Contr. U. S. Nat. Herb. **19**: 300. 1915. — Bean, Trees Shrubs **2**: 139. 1914; **ed. 7, 2**: 416. 1950; et in Chitt., Dict. Gard. **3**: 1546. 1951. — Moore in Bailey, Stand. Cycl. Hort. **5**: 2582. 1916. — Rehder, Man. Cult. Trees Shrubs 279. 1927; ed. 2, 273. 1940; et Bibl. Cult. Trees Shrubs 194. 1949. — Engler, Pflanzenf. ed. 2, **18a**: 193. 1930. — Tid. & Kitt., Fl. Ariz. N. Mex. 262. 1941. — McDougall and Sperry, Plants 88. 1947.

Philadelphus microphyllus var. *typicus* Koehne, Dendr. 185. 1893. — Schneider, Ill. Handb. Laubh. **1**: 365. 1905.

Philadelphus microphyllus subsp. *typicus* Hitchc. in Madroño **7**: 49. 1943. — Kearn. & Peebles, Ariz. Fl. 367. 1951.

TYPE: *A. Fendler 266* (G).

A low, erect shrub up to a meter high with rather loose branches; bark of the second year's growth chestnut brown, shiny, exfoliating, the exposed portion ochraceous, striate, the current year's growth sparsely villose, the hairs all appressed; the flowering twigs 1.5–3, rarely up to 5 cm. long, with 3 or 4 pairs of leaves, the axillary buds enclosed. Leaves ovate-elliptic, elliptic or rarely sublanceolate, 1–1.5 cm. long, 5–7 mm. wide, entire and ciliate, when dry brown and glabrescent above, pale olive-brown, softly long-villose on the nerves or sometimes sparsely villose all over beneath, obtuse at the base, acute or obtuse at the apex, the petioles 2 mm. long, weakly villose. Flowers solitary, rarely 2, terminal, subtended by linear leaves; hypanthium campanulate, more or less villous at the base and sparsely so at the angles, the major part of the hypanthium and calyx glabrous, the sepals ovate-lanceolate, 5 mm. long, 3 mm. wide at the base; corolla cruciform, 3 cm. across, the petals obovate-oblong, rounded and erose at the apex, 1.5 cm. long, 9 mm. wide; stamens ca. 32, the filaments all distinct; disc and style glabrous, the style 1 mm. long, the upper third distinct, the stigmata 2 mm. long. Capsules globose, 7 mm. in diameter, the persistent calyx circumferential. Seeds ellipsoid, 2 mm. long including the tail, the testa castaneous, striately reticulate, the tail very short, about one eighth the length of the embryo.

UNITED STATES: **Colorado:** Fremont Co., Oak Creek Canyon, *R. C. Rollins 1240* (G, MO, NY, US); Grand Canyon, Arkansas, *G. Engelmann & C. S. Sargent*, June 25, 1880 (A); Las Animas Co., Branthy Canyon, *G. E. Osterhout 2077* (NY); Mesa Verde National Park, *H. L. Zobel*, July 1, 1935 (MO). **Arizona:** Apache Co., Chile, *H. C. Cutler 2158* (G, MO); Luka Chukai Mt., *G. J. Goodman & L. P. Payson 2843* (G, MO, NY); Navajo Reservation, *P. C. Standley 7323* (US); *C. T. Vorhies 109* (G); University of Arizona Herbarium, July 1916 (A, MO, NY). **Utah:** Carbon Co., Cottwood Canyon, *E. H. Graham 9520* (MO); Grand Co., Post Canyon, *E. H. Graham 9916* (F, G, MO); Moab, *M. E. Jones*, June 1, 1915 (NY); Wilson Mesa, *P. A. Rydberg & A. O. Garrett 8380* (NY); La Sal Mt., *Maguire, Richard, Maguire & Hammond 5803* (G, MO); Wayne Co., *H. Dixon 205* (F). **Nevada:** Clark Co., Deadman's Canyon, *A. M. Alexander & L. Kellogg 1785* (G, US); Lee Canyon, *I. W. Clokey 8393* (A, NY). **New Mexico:** Bernalillo Co., Sandia Mts. Balsam Park, *C. C. Ellis 107* (MO, NY, US); Cenigua Canyon, *Sister M. Marcelline 2673* (F); Albuquerque, *E. J. Palmer 31176* (A); Ellis Ranch, *E. O. Wooton*, Aug. 3, 1910 (US); Colfax Co., Ute Park, *P. C. Standley 13295* (US); Pecos River National Forest, *P. C. Standley 4547* (G, MO, NY, US); Sandoval Co., Sandia Mts., Guadalupe Canyon, *W. W. Eggleston 18736* (US); Santa Fe Co., Santa Fe, *Bro. G. Arsène & Bro. A. Benedict 15741* (F), *15742* (F, US); same area, *C. S. Sargent*, Sept. 4, 1894 (A); Santa Fe Creek, *A. Fendler 266* (G, TYPE; A, F, NY, US, ISOTYPES); Santa Fe Canyon, *A. A. & Gertrude Heller 3792* (A, F, G, MO, NY); *E. O. Wooton*, Aug. 6, 1910 (US); Santa Clara Canyon, *Sister M. Marcelline 1852* (F); Water Canyon, *M. C. Wiegand & G. B. Upton 3424* (F); Rito de las Frigales, *T. D. A. Cockerell*, Aug. 1912 (US); Socorro Co., San Mateo Mts., Beartrap Canyon, *W. W. Eggleston 18654* (NY, US); San Mateo Peak, *E. A. Goldman 1745* (US); Magdalena Mts., Water Canyon, *C. J. & Ruth Herrick*

202 (F); Taos Co., Taos River Canyon, *A. Nelson 11471* (G). **Texas:** Brewster Co., Chisos Mts., *R. S. Ferris & C. D. Duncan 2856* (MO, NY); *E. G. Marsh 101* (F); *J. A. Moore & Steyermark 3160* (A, G, MO); *C. Mueller 8013* (A, F, MO); *B. H. Warnock 866* (G, US).

CULTIVATED: Europe: Bot. Gard. Wien, *C. Schneider*, June 18, 1902 (A); Hort. Götting, *A. Rehder*, June 15, 1893 (A), June 25, 1896 (A); Bot. Gart. Forstakadamie, Muenden, Hannover, *H. Zabel*, Aug. 23, 1884 (A), June 28, 1895 (A). United States: Arnold Arb. *544*, June 27, 1904 (A).

This species was discovered in 1847 and as early as 1883 was introduced to Europe through the Lemoine Nursery in Nancy, France. I have examined a specimen of one of the earliest cultivated plants. It was collected by H. Zabel on Aug. 23, 1884 from the Botanischer Garten der Forstakadamie, Muenden, Hannover. A note on this specimen, "Lemoine, 1883," indicates the approximate date and agent of the introduction of the species to Europe. Its dwarf habit and its apple-quince scented fragrance gave it popularity among growers there. By 1887 it could be found in many outstanding botanical gardens. Nicholson of Kew published an illustrated account of it in the Gardener's Chronicle. That same year a colored plate of it appeared in the Wiener Illustrierte Garten-Zeitung, which indicates its cultivation in Austria. By 1912 it was also reported to grow in gardens in Scotland. In the meantime European hybridists have taken advantage of its low compact habit and its pleasing fragrance. In 1887 the Lemoine Nursery put into the trade a new hybrid, *P. lemoinei*, which was announced as the result of a cross between the European *P. coronarius* Linn. and the American *P. microphyllus* Gray.

This species was first collected in the Santa Fe Creek of New Mexico. Its range extends north to the southern Rocky Mountains, west and northwest to the canyon lands and the Navajo section of the Colorado plateaus, reaching the Arizona portion of the Sonoran Desert, and south to the Texas portion of the Mexican highland. In the northern area of this range it has been reported to occur among *Juniperus* and *Pinus* at altitudes of 1540–2440 meters. There it grows in dry places at the base of granite cliffs or sandstone canyons, and its white, fragrant flowers appear in late June to mid-July. In New Mexico it grows at altitudes from 2200 to 3050 meters. In the southern portion of its range it has been reported to occur along dry streamlets at altitudes of about 1830 meters, and its flowers appear in June.

The type specimen of this species has small ovate-elliptic, elliptic, or even sublanceolate leaves which are obtuse at the base and almost glabrous on the upper surfaces. It has cruciform flowers with oblong petals which are about 1.5 cm. long. The specimens cited above possess these common features. Among the representatives of the wild population which I have examined, there are two varieties which can be recognized by their exceedingly narrow or unusually broad leaves. The leaves of these varieties are uniformly strigose or pilose above. In the broad-leaved form the corolla of the flowers is disciform and the petals are suborbicular.

KEY TO THE VARIETIES OF *P. microphyllus*

A. Leaves linear-lanceolate, 2–3 mm. wide ..... var. *linearis*.
AA. Leaves ovate, 6–15 mm. wide, rounded at the base ..... var. *ovatus*.

50a. **Philadelphus microphyllus** var. **linearis**, var. nov.

Frutex, ramis cinereis, hornotinis castaneis, pilosis, deinde exfoliatis; foliis lanceo-linearibus, 10–16 mm. longis, 2–3 mm. latis, utrinque obtusis, supra tenuiter strigosis, subtus strigosis; hypanthiis calycibusque glabris vel glabrescentibus; disco glabro, stylo 2 mm. longo, stigmatibus 2.5 mm. longis, divisis.

ARIZONA: Tunitcha Mts., *E. A. Goldman 2928* (TYPE, US).

This variety is distinguished from the typical *P. microphyllus* Gray by its linear leaves, which are uniformly 2–3 mm. wide and more or less strigose on both surfaces.

50b. **Philadelphus microphyllus** var. **ovatus**, var. nov.

Frutex, ramis cinereis, hornotinis castaneis, dense pilosis, deinde exfoliatis; foliis ovatis, 8–28 mm. longis, 6–15 mm. latis, basi rotundatis, apice obtusis, supra uniforme pilosis, subtus strigosis, vel villosis; floribus solitariis vel ternatis, hypanthiis basi pilosiusculis, sepalis glabris, corolla disciformi, 1.5–2.5 cm. diametro, petalis suborbicularibus, 6–10 mm. diametro; staminibus ca. 35; disco et stylo glabris; stylo 2 mm. longo, stigmatibus 3 mm. longis, divisis.

UNITED STATES: **Colorado:** Las Animas Co., northern slope of Mesa de Maya, *R. C. Rollins 1835* (MO, NY, US). **Arizona:** Tunitcha Mts., *E. A. Goldman 2913* (US). **Utah:** Grand Co., Moab, *M. E. Jones*, June 8, 1913 (F, G, NY, US); Juab Co., La Sal Mt., *C. A. Purpus 6611* (MO, US); Marvin Laccolita, *M. E. Jones 5663v* (MO, NY, US); San Juan Co., *P. A. Rydberg & A. O. Garrett 9608* (US); Uintah Co., Ashley Creek, *E. H. Graham 6270* (MO, US). **New Mexico:** Bernalillo Co., Sandia Mts., *C. L. Herrick*, June 30, 1898 (US); Sierra Co., Hillsboro Peak, *O. B. Metcalfe 1323* (A, TYPE; F, G, US, ISOTYPES); Socorro Co., Magdalena Mts., Copper Canyon, *E. A. Goldman 1669* (US); Valencia Co., mountains west of Grant station, *E. O. Wooton 1109* (NY, US).

This variety differs from the typical *P. microphyllus* Gray in its broader leaves, which are ovate and uniformly pilose above, and in its disciform corolla with suborbicular petals.

51. **Philadelphus argyrocalyx** Wooton in Bull. Torr. Bot. Club 25: 452. 1898. — Koehne in Mitt. Deutsch. Dendr. Ges. 1904 (13): 78. 1904. — Rydb. in N. Am. Fl. 22: 171. 1905. — Jones in Contr. West. Bot. 13: 11. 1910. — Standley in Contr. U. S. Nat. Herb. 13: 190. 1910. — Wooton & Standley in Contr. U. S. Nat. Herb. 19: 300. 1915. — Rehder, Man. Cult. Trees Shrubs 279. 1927; ed. 2. 273. 1940; et Bibl. Cult. Trees Shrubs 194. 1949. — Tid. & Kitt., Fl. Ariz. N.

Mex. 262. 1941. — Bean, Trees Shrubs ed. 7, 2: 411. 1950; et in Chitt., Dict. Gard. 3: 1545. 1951.

Philadelphus serpyllifolius var. Gray, Pl. Wright. 2: 64. 1853.

Philadelphus ellipticus Rydb. in N. Am. Fl. 22: 172. 1905. — Standley in Contr. U. S. Nat. Herb. 13: 190. 1910. — Wooton & Standley in Contr. U. S. Nat. Herb. 19: 300. 1915.

Philadelphus serpyllifolius var. *argyrocalyx* (Wooton) Jones in Contr. West. Bot. 12: 14. 1908.

Philadelphus microphyllus ssp. *argyrocalyx* (Wooton) Hitchc. in Madroño 7: 45. 1943, pro parte. — Kearn. & Peebles, Ariz. Fl. 367. 1951.

TYPE: *E. O. Wooton 524* (US).

An erect shrub 1–2 m. tall, the branchlets grayish brown, fibrously striate, the second year's growth brown or castaneous, the bark closed, tardily exfoliate, the current year's growth brown, ferrugineous-villose, the hairs slightly thickened at the base, axillary buds enclosed. Leaves ovate, ovate-lanceolate or elliptic, 1–3.5 cm. long, 4–15 mm. wide, obtuse at the base, acute or obtuse at the apex, glabrous or glabrescent above, uniformly sparse strigose-villose beneath, the hair more or less erect, the petioles 1.5–2.5 mm. long, villose, the hair white. Flowers solitary, the pedicels 1–2 mm. long, densely long-villose; hypanthium subcampanulate, with the calyx thickly lanate, the sepals ovate-lanceolate, 7–8 mm. long, 3.5–4.5 mm. wide at the base, acuminate at the apex; corolla cruciform, 3.5 cm. across, the petals ovate-oblong, 15–17 mm. long, 10–14 mm. wide, rounded and emarginate at the apex; stamens ca. 55, the filaments united into bundles; disc and style glabrous, the style 3 mm. long, the stigmata 3.5 mm. long, the upper half separated, the fertile surface abaxial, linear. Capsules oblong-subglobose, 10–12 mm. long, 7–9 mm. in diameter, the persistent calyx circumferential. Seeds rather large, including the tail 3–4 mm. long, the testa castaneous, striately reticulate, the tail rather long, equal to or slightly shorter than the embryo.

UNITED STATES: **New Mexico:** Lincoln Co., White Mts., *E. O. Wooton*, June 30, 1895 (NY, US, PARATYPE); Eagle Creek, *E. O. Wooton 524*, Aug. 14, 1897 (US, TYPE); Nogal Canyon, *E. O. Wooton*, Aug. 17, 1901 (US); *L. C. Hinckley 1026* (F); El Capitan Mts., *F. S. & E. S. Earle 220* (MO); Otero Co., Lincoln Forest, *W. W. Eggleston 14541* (US); Mesilla Park, *J. D. Tinsley* in 1896 (US, TYPE of *P. ellipticus* Rydb.; NY, photo and fragment); vicinity of Cloudcroft, *E. O. Wooton*, July 29, 1899 (US); Sacramento Mts., Cloudcroft, *A. Rehder 372* (A); between Alamogordo and Cloudcroft, *A. Rehder 315* (A); Nogal Canyon, *W. Huber*, July 1, 1931 (F); Alamo National Forest, Head of Rio Fresnal, *B. Barlow*, Aug. 12, 1911 (F).

CULTIVATED: Arnold Arboretum *9044*, *A. Rehder*, Oct. 1, 1918 (A), July 2, 1919 (A), July 20, 1927 (A).

Available material indicates that *P. argyrocalyx* Wooton has a very limited range of distribution. It is endemic to the isolated block mountains of south central New Mexico. There at altitudes of 2440–2590 meters it

is found as a shrub about one or two meters high. Its fragrant white flowers appear from late June to mid-August.

In the publication of this species Wooton cited four collections, but did not designate a type. Seventeen years later, in a joint work with Standley, he definitely indicated his second collection, numbered *524*, as the type. This specimen was collected on Aug. 14, 1897. It was in fruit. Flowering material in the New York Botanical Garden bears on its label the same legend. This specimen is apparently not an isotype. It is probably a part of Wooton's first collection dated June 30, 1895, which is a paratype of this species. The other two specimens Wooton cited became the type material of *P. argenteus* Rydb.

Rehder 372 also consists of different elements. Under this number one sheet in the Arnold Arboretum is a flowering specimen. It is true to the type of *P. argyrocalyx*. Under the same number there is another sheet in the Arnold Arboretum and one in the U. S. National Herbarium which are fruiting specimens. The capsules are evidently developed from flowers with pubescent discs. The seeds have short tails.

The glabrescent leaves and the large subcruciform flowers of *P. argyrocalyx* Wooton indicate its close affinity to *P. microphyllus* Gray. It can easily be distinguished from the latter species by its thickly lanate hypanthium and calyx. Its long-tailed seeds and oblong subglobose capsule with the circumferential persistent calyx suggest some kinship with *P. inodorus* Linn., but this relationship is rather distant. The character of connate filaments suggests a relationship with *P. palmeri* Rydb. It is highly probable that it is through these two species that a Mexican element, *P. maculatus* (Hitchc.) S. Y. Hu, is linked with the northern element *P. microphyllus* Gray.

This species was introduced into cultivation by A. Rehder, who in Aug. 1916 collected some seed from the south slope of the Sacramento Mountains near Cloudcroft, New Mexico. Plants from that lot of seed cultivated under the Arnold Arboretum field number *9044* flowered in early July 1919. Boston weather did not seem to alter the specific characters of this taxon. The density of the indumentum on the leaves and hypanthium, the shape of the corolla, the connate filaments, and the glabrous style of the cultivated specimen all resemble the type material. Through successive cuttings that introduction had been kept in the Arnold Arboretum for thirty years. Unfortunately the last plant was discarded in 1944. The plant now growing in the Arnold Arboretum under this specific name is one introduced from Kew in 1945.

52. **Philadelphus wootonii**, sp. nov.

Frutex ramulis castaneis, tarde exfoliatis, bienniis dense pilosis, hornotinis tomentosis, gemmis axillaribus tectis; foliis ovatis, 10–18 mm. longis, 5–9 mm. latis, utrinque acutis vel obtusis, supra sparse villosis, subtus dense strigoso-villosis, pilis erectis, petiolis 2 mm. longis, villosis; floribus solitariis, pedicellis 1–3 mm. longis, cum hypanthiis calycibusque lanatis.

hypanthiis subcampanulatis, sepalis ovatis, 3–4 mm. longis, basi 3 mm. latis; corolla subdisciformi, 2 cm. diametro, petalis ovatis, 8 mm. longis, 6–7 mm. latis; medio disci et basi styli hirsutis, stylo 2 mm. longo, stigmatibus 3 mm. longis, dimidiis apicibus divisis; capsulis subgloboso-ellipsoideis, 7–8 mm. longis, 6–7 mm. diametro, calycibus persistentibus circumferentibus; seminibus breviter caudatis, cum caudis 3 mm. longis, testis castaneis, striato-reticulatis.

NEW MEXICO: White Mts., Gavilan Canyon, *E. O. Wooton*, July 23, 1905 (US, TYPE); Sacramento Mts., Cloudcroft, *A. Rehder 372* (A, US, fruit).

Both in appearance and range this species appears to be similar to *P. argyrocalyx* Wooton. Apparently they are closely related species, though they can be easily distinguished. *Philadelphus argyrocalyx* Wooton has cruciform flowers, glabrous disc and style and long-tailed seeds. *Philadelphus wootonii* has disciform flowers, pubescent center on the disc and base of the style, and short-tailed seeds. The inclosed buds and the short-caudate seeds indicate that *P. wootonii* is a species of the *microphyllus* type which is somewhat influenced by the *mexicanus* or *coulteri* type with pubescent disc and style.

53. **Philadelphus occidentalis** Nelson in Bull. Torr. Bot. Club **25**: 374. 1898. — Koehne in Mitt. Deutsch. Dendr. Ges. **1904** (13): 79. 1904. — Rydb. in N. Am. Fl. **22**: 173. 1905.

Philadelphus microphyllus subsp. *occidentalis* (Nelson) Hitchc. in Madroño **7**: 51. 1943, pro parte. — Kearn. & Peebles, Ariz. Fl. 367. 1951.

Philadelphus microphyllus subsp. *stramineus* forma *zionensis* Hitchc., op. cit. 48.

TYPE: Wyoming, *R. A. Smith, Jr. 3595* (Rocky Mountain Herb.).

A low shrub, the branches ochraceous, longitudinally fibrous-striate, the second year's growth castaneous, exfoliate, the current year's growth inconspicuously pilose, the hairs appressed. Leaves ovate or oblong-ovate, 10–20, rarely up to 25 mm. long, 5–11 mm. wide, obtuse or rounded at the base, obtuse or acute at the apex, entire, uniformly sparsely strigose-pilose on both surfaces, the hairs appressed. Flowers solitary or ternate, the pedicels 2 mm. long, strigose and incanous; hypanthium and sepals uniformly strigose-pilose, the epidermal tissue not obscured, the hairs appressed; sepals ovate, 4–6 mm. long, the apex acuminate; corolla disciform, 15–25 mm. across, the petals obovate, 5–10 mm. long, 4–8 mm. wide, the apex rounded; stamens ca. 35; disc and style glabrous, the style 1 mm. long, the stigma linear, 1.5 mm. long, slightly divided at the tip. Capsules subglobose-ellipsoid, 5 mm. long, 4.5 mm. in diameter, slightly pointed at both ends, the persistent sepals subapical. Seeds short-caudate, small, with the tail 1.5–2 mm. long, the testa light brown.

UNITED STATES: **California:** Inyo Co., Panamint Mts., Death Valley, *F. V. Coville & M. F. Gilman 24* (US), *95* (US), *213* (US); Inyo Mts., Cerro Gordo

Peak, *A. M. Alexander & L. Kellogg 3038* (G, US), White Mts., Wyman Creek, *I. Tidestrom 9885* (A); same locality, *B. Maguire & A. H. Holmgren 26038* (G, NY, US). **Wyoming:** Sweetwater Co., Rock Springs, *A. Nelson 3595*, July 15, 1897 (G, NY, US, ISOTYPES), July 15, 1898 (MO, US); same locality, *R. A. Smith 6919* (G, MO, NY, US, ISOTYPE?). **Colorado:** Fremont Co., Royal Gorge, *R. Bacigalupi 1009* (G, NY); same locality, *I. W. Clokey 3791* (F, G, MO, NY, US); Arkansas Cañon, *J. H. Redfield 456* (NY); Cañon City, *T. S. Brandegee 84* (NY), June 1877 (F, NY); Garfield Co., Glenwood Spring, *E. J. Palmer 38115* (A, F, MO, NY, US); *F. Wislizenus 1041* (MO); *E. B. Payson 1197* (MO); New Castle, *M. Cary 153* (US); Gunnison Co., southwest of Sapinero, *R. C. Rollins* 51170; Moffat Co., confluence of Green & Yampa Rivers, *C. L. Porter 3619* (G, US); Mesa Co., Gateway, *B. Maguire & G. Piranian 12426* (G); Royal Gorge, *E. B. Payson 1023* (MO); Gunnison Canyon, *E. B. Payson 1056* (MO); Mesa Verde National Park, *E. B. Payson 1137* (MO); Montrose Co., Grand Canyon, *F. H. Knowlton 258* (US); Park Co., Webster Park, *E. A. Popenoe*, July 30, 1876 (MO, US); Colopasi, *E. L. Johnston & G. G. Hedgcock 740* (NY); without precise locality, *D. E. Palmer 309* (US); *H. D. Ripley & R. C. Barneby 7157* (NY). **Utah:** Belknap, *S. G. Stokes*, June 12, 1900 (NY); Daggett Co., Manila, *B. Maguire & G. Piranian 12379* (G); below Ashley Falls in Red Canyon of the Green River, *H. Cutler & M. Baker* (G, MO, NY); Gronse, *E. H. Graham 8091* (MO); Grands Co., Thompson's Springs, *M. E. Jones* (G, US); Juab Co., Deep Creek Ranges, *B. Maguire & A. H. Holmgren 21864* (G, MO, NY); Piute Co., Marysvale, *M. E. Jones 3575p* (US), *5405j* (US), *5904d* (NY, US); Sevier Co., Burrville Canyon, *M. E. Jones 5633* (A, NY, US); San Juan Co., *P. A. Rydberg & A. O. Garrett 9609* (NY, US); Uintah Co., *A. O. Garrett 7837* (F); Uintah Mts., Brush Creek Canyon, *L. N. Goodding 1274* (G, NY); Uinta Basin, *E. H. Graham 7454* (G, MO), *9145* (MO), *10015* (MO); Vernal, *B. F. Harrison & Larsen 7761* (MO); Washington Co., Zions Canyon, *A. O. Garrett R2269* (NY); *L. F. Ward 699* (US); Zion National Park, *A. M. Woodbury 19* (US); *O. Degener & L. Peiler 16550* (NY); Warner Ranger Station, *Maguire et al. 5802* (US). **Nevada:** Clark Co., Deadman's Canyon, *A. M. Alexander & L. Kellogg 1779* (G). **Arizona:** Coconino Co., Grand Canyon, *W. P. Cottam 2669* (A); *H. & V. Bailey 1226* (A); Graham Co., Chiricahua Mts., *J. C. Blumer 1303* (F, G, NY); Mohave Co., Grand Canyon, *J. W. Toumey 133* (US); Santa Cruz Co., Huachuca, *L. N. Goodding 147* (G, NY); Santa Rita Mts., *C. G. Pringle*, June 3, 1881 (F, US), July 13, 1881 (A, NY), June 2, 1884 (F); San Pedro River, *E. A. Mearns 1540* (US); N. Arizona–S. Utah, *D. E. Palmer 151* (G, MO, NY, US). **Texas:** Brewster Co., Chisos Mts., *V. L. Cory 7077* (G); *V. Havard 40* (G, US). **New Mexico:** Socorro Co., Hop Canyon of Magdalena Mts., *C. L. Herrick 608* (US); Animas Peak, *E. A. Goldman 1370* (US).

MEXICO: Chihuahua: San Luis Mts., Devil's Canyon, *E. A. Goldman 1432* (US). Baja California: Sierra San Pedro Martir, *B. V. Meling*, July 30, 1931 (US).

In designating the type Nelson stated, "Collected first by the writer, but the excellent specimens, which are taken as the type, were secured by Robert Smith, Jr., from the same locality July 25, 1897, no. *3595*." With the type material of this species distributed by the Rocky Mountain Herbarium, University of Wyoming, Laramie, I have seen three specimens with the following data: July 15, 1897, *Aven Nelson 3595*; July 15, 1898,

Aven Nelson 3595; July 1899, *R. A. Smith 6919*. None of these data agrees with Nelson's publication.

Philadelphus occidentalis is closely related to *P. microphyllus* Gray. It can be distinguished readily by its uniformly loose strigose-pilose hypanthium and its disciform corolla. In *P. microphyllus* the hypanthium is almost glabrous and the corolla cruciform.

53a. **Philadelphus occidentalis** var. **minutus** (Rydb.), stat. nov.

Philadelphus minutus Rydb. in N. Am. Fl. **22**: 173. 1905.

Philadelphus microphyllus subsp. *occidentalis* Hitchc. in Madroño **7**: 51. 1943, pro parte.

Philadelphus nitidus Nelson in Bot. Gaz. **42**: 54. 1906. — Longyear, Trees Shrubs Rocky Mt. Reg. 124. 1927.

TYPE: Colorado: *C. F. Baker 266* (NY).

A divergently branched low shrub, the second year's growth castaneous, shiny, tardily exfoliate; leaves oblong to oblong-lanceolate, acute or obtuse at both ends, 10–17 mm. long, 2–5, rarely up to 7 mm. wide, very sparsely strigose-pilose above, uniformly strigose-pilose beneath, hairs appressed; flowers solitary, the corolla subcruciform, 13–17 mm. across, the petals oblong, 6–8 mm. long, 4–5 mm. wide; capsules small, subglobose, 4 mm. in diameter.

UNITED STATES: **Colorado:** Black Canyon, *C. F. Baker* (NY, TYPE; G, MO, US, ISOTYPES); same locality, *C. A. Purpus 511* (F); Grand Canyon National Park, *M. Gilstrap 13* (US). **Utah:** Sevier Co., Belknap, *M. E. Jones 6303* (MO, NY, US, PARATYPE of *P. nitidus* Nelson); without precise locality, *P. V. LeRoy 151* (NY). **Nevada:** Clark Co., Deer Creek, *I. W. Clokey 5485* (A, NY); Charleston Mountains, Lee Canyon, *A. A. Heller 10998* (A, F, G, MO, NY).

This variety can readily be distinguished from the typical *P. occidentalis* by its oblong-lanceolate leaves. Nelson observed this leaf character and described *P. nitidus* in 1906. One of his paratypes, *C. F. Baker 266*, was the type of an early binomial, *P. minutus* Rydb. Besides its narrow leaves, I can detect no appreciable difference between Rydberg's *P. minutus* and Nelson's *P. occidentalis*. I think Rydberg's species can be regarded only as a narrow-leaved variety of *P. occidentalis*.

54. **Philadelphus argenteus** Rydb. in N. Am. Fl. 22: 171. 1905. — Tid. & Kitt., Fl. Ariz. N. Mex. 262. 1914.

Philadelphus argyrocalyx var. *argenteus* (Rydb.) Engler, Pflanzenf. ed. 2, **18a**: 193. 1930.

Philadelphus microphyllus var. *argenteus* (Rydb.) Kearn. & Peebles in Jour. Wash. Acad. Sci. **29**: 480. 1939.

Philadelphus microphyllus ssp. *argenteus* (Rydb.) Hitchc. in Madroño **7**: 42. 1943. — Kearn. & Peebles, Ariz. Fl. 367. 1951.

Philadelphus microphyllus ssp. *stramineus* (Rydb.) Hitchc. in op. cit. 47. 1943, pro parte. — Clokey in Univ. Calif. Publ. Bot. **24:** 109. 1951, pro parte.

TYPE: *T. E. Wilcox*, July 1893, Fort Huachuca, Arizona (NY).

A xerophytic shrub, 1–2 m. high, branchlets gray, the second year's growth castaneous, slowly exfoliating, the current year's growth incanous. Leaves ovate or elliptic-oblong, 8–16 mm. long, 4–10 mm. wide, acute or obtuse at both ends, rarely the lower leaves of a branchlet rounded at the apex, uniformly weak-strigose above, incanous beneath, the hairs largely strigose, mixed with some crisp weakly villose ones, all appressed, the petioles 1–1.5 mm. long, incanous. Flowers solitary, the pedicels 1–1.5 mm. long, with the hypanthium and calyx incanous, the hairs largely strigose, appressed, obscuring the epidermis, the sepals deltoid, 5 mm. long, 4 mm. at the base, the apex acuminate; corolla disciform, 1.5–2.4 cm. across, the petals ovate, 6–10 mm. long, 5–10 mm. wide, sometimes sparsely pilose at the base outside; stamens ca. 46, the filaments separated; disc and style glabrous, the style 1 mm. long, the stigmata 4 mm. long, the upper third or half divided at anthesis. Capsules ellipsoid, 6 mm. long, 5 mm. in diameter, the persistent calyx subapical. Seeds oblong-ellipsoid, including the tail 2 mm. long, testa castaneous, striately reticulate, the tail very short, about one eighth the length of the embyro.

UNITED STATES: **California:** Inyo Co., Cerro Gordo Peak, *A. M. Alexander & L. Kellogg 3038* (A), *3115* (A); same locality, *M. Kerr 619* (A); Mono Co., White Mts., Black Canyon, *V. Duran 540* (F, G, MO, NY); Riverside Co., San Jacinto Mts., *P. A. Munz 8738* (G). **Colorado:** Grand River Canyon, Biltmore Herb. no. *5330* (A); Grape Creek Canyon, Herb. *E. A. Popenoe 115* (A). **Utah:** Burrville Canyon, *M. E. Jones 5633* (A, F, MO, NY). **Nevada:** Clark Co., Kyle Canyon, *I. W. Clokey 5490* (NY); Griffith's Mine, *I. W. & C. B. Clokey 7133* (NY); Deer Creek, *I. W. Clokey 7540* (CU, F, MO, NY, US); same locality, *P. Train 2178* (NY); Lee Canyon, *A. A. Heller 10998* (A, US), *I. W. Clokey 8486* (A, NY); Little Falls, *I. W. Clokey 5487* (A); Trout Canyon, *P. Train 2061* (A). **Arizona:** S. Colorado Mts., *J. G. Lemmon 170* (G); Grand Canyon, *A. E. Hitchcock 91* (US); Patagonia, *G. J. Harrison 7180* (NY); Cochise Co., Bisbee, *J. I. Carlson*, May 31, 1913 (A, US); Fort Huachuca, *T. E. Wilcox*, June 1892 (NY), July 1893 (NY, TYPE; A, ISOTYPE), July 1894 (A, US); Superstition Mts., *G. J. Harrison 6604* (NY); Santa Cruz Co., Santa Rita Mts., *C. G. Pringle 13685* (G, NY). **Texas:** Trans-Pecos, *B. C. Tharp 1439* (US); Brewster Co., Old Blue Grass Mts., *B. H. Warnock 20894* (G); Culberson Co., Guadalupe Mts., McKittnick Canyon, *J. A. Moore & J. A. Steyermark 3479* (A, G, MO, NY, US); Hudspeth Co., Sierra Blanca, *U. T. Waterfall 6713* (G, MO); Jeff Davis Co., Davis Mts., Mt. Livermore, *L. C. Hinckley 50* (F), *1170* (F), Aug. 27, 1939 *s.n.* (G); *E. J. Palmer 34292* (A).

MEXICO: Baja California: Sierra San Pedro Martir, *I. L. Wiggins & D. Demaree 4947* (F, NY, US); same locality, *E. A. Goldman 1223* (US). Sonora: San Jose Mts., *E. A. Mearns 1617* (US).

This species was first discovered at Fort Huachuca in southeastern Arizona. Its range, as indicated by additional collections, extends north-

eastward to the Sonoran Desert of southern Nevada and to the Sierra Nevada of eastern central California, northward to the Grand Canyon in Arizona and to central Utah and western Colorado, and southeastward to western Texas. Judging from the specimens I have examined, the center of concentration for this species is on the western and southeastern sections of its range. I have seen only a few specimens from the northern and eastern portions of this area.

In California it has been reported as a common shrub and grows on the ridges of the San Jacinto Mountains. In Nevada it has been reported to occur at altitudes between 2370 and 2750 meters. There it grows on gravelly hillsides among pines and junipers or on limestone cliffs. Its fragrant white flowers appear in July and August. In Arizona it occurs at altitudes between 2100 and 2800 meters, where flowering specimens have been collected in July. In Texas it occurs at altitudes between 2100 and 2300 meters, where flowering specimens have been collected as late as August.

From the type locality, Fort Huachuca, T. E. Wilcox collected specimens in June 1892, July 1893, and June 1894. The last-dated specimen in the United States National Herbarium is numbered *234*. The other two are not numbered. His 1893 collection, deposited in the New York Botanical Garden, is the taxonomic type of the species.

The taxonomic status of *P. argenteus* Rydb. has been changed several times in the last fifty years. Engler interpreted it as a variety of *P. argyrocalyx* Wooton. Kearney and Peebles treated it as a variety of *P. microphyllus* Gray, and Hitchcock made it a subspecies of the latter. The differences existing between *P. argenteus* Rydb. and *P. microphyllus* Gray are comparable to those existing between *P. pubescens* Loisel. and *P. lewisii* Pursh. In both cases, there is a species with densely pubescent leaves, incanous hypanthium and pubescent calyx, and another species with these parts glabrous or glabrescent.

The affinity between *P. argenteus* Rydb. and *P. argyrocalyx* Wooton is closer, but they are distinct species. Both have white-hoary hypanthia and calyx. But the nature and density of the indumentum of these two species are very different. In *P. argenteus* the lower surface of the leaves is densely strigose with straight appressed hairs, covering some weaker crisp hairs, and the upper surface is strigose. The incanous hypanthium of this species has straight appressed hairs. In *P. argyrocalyx* the lower surface of the leaves has loosely arranged long-villose hairs, and the upper surface is glabrescent. The lanate hypanthium has woolly hairs. The leaves of *P. argyrocalyx* Wooton are in general much larger, measuring up to 3 cm. long.

The Nevada specimens cited above have been interpreted by Hitchcock & Clokey as *P. microphyllus* Gray ssp. *stramineus* Hitchc.

55. **Philadelphus palmeri** Rydb. in N. Am. Fl. 22: 173. 1905.

Philadelphus microphyllus ssp. *argenteus* (Rydb.) Hitchc. in Madroño 7: 42. 1943, pro parte.

Philadelphus madrensis sensu Standl. in Contr. U. S. Nat. Herb. **23**: 310. 1922, pro parte, non Hemsl.

TYPE: Mexico, Sierra Madre, *Edward Palmer 2122* (G).

A shrub with fibrous gray branchlets, the second year's growth grayish brown, exfoliating, the current year's growth strigose-villose, the base of the hairs more or less thickened, axillary buds enclosed. Leaves lanceolate, 10–30 mm. long, 3–11 mm. wide, acute at the base, acute or subacuminate at the apex, uniformly sparse-pilose above, the hair appressed, densely strigose-pilose beneath, the hairs largely straight and mixed with some weak and crisp ones, all appressed, the petioles 1.5–2 mm. long, incanous. Flowers solitary, the pedicels 4 mm. long, with the hypanthium and calyx incanous, the hair all straight and appressed; sepals ovate, 5 mm. long, 3.5 mm. wide at the base, the apex acute; corolla subcampanulate, 2–2.5 cm. across, the petals oblong-obovate, 10 mm. long, 5–8 mm. wide, stamens ca. 23, the filaments united in 5 or more bundles, the disc and style glabrous, the style 1.25 mm. long, the stigmata 2–2.5 mm. long. Capsules turbinate, 4–7 mm. long, 5–7 mm. in diameter, the persistent calyx subapical. Seeds oblong ellipsoid, with the tail 2 mm. long, about one eighth the length of the embryo, the testa castaneous, striately reticulate.

UNITED STATES: **Arizona:** Chiricahua National Forest, *H. D. Burrall 2079* (US), Chiricahua Mts., Cave Creek Canyon, *J. A. Kusche*, July 1927 (A). **Texas:** Mt. Livermore, L. C. Hinckley *1162* (F).

MEXICO: Coahuila: Sierra Madre, 40 miles south of Saltillo, *Edward Palmer 2122* (G, TYPE; MO, ISOTYPE); Sierra de la Madera, Cañon del Agua, Cuatro Cienegas, *C. H. Muller 3230* (A); Sierra de Parras, *C. A. Purpus 4952* (F, G, MO, US); Nuevo Leon: Sierra Madre Oriental, Zaragoza, *F. G. Meyer & D. J. Rogers 2993* (A, MO); Fraile, *Stanford, Retherford & Northcraft 388* (A, MO).

Among the above-cited five collections, *Stanford et al. 388* matches the type best. *Muller 3230*, on which the description of the fruits and seeds of the species is based, has broader leaves and looser indumentum. On the contrary, *Purpus 4952* has much smaller leaves and denser tomentum. As a few broad leaves, like those of Muller's collection occur also on some healthy vegetative shoots of *Stanford et al. 388*, and a few small leaves like those of Purpus' collection are found also on the weak vegetative shoots of the same number, I have no doubt of the identity of *Muller 3230* and *Purpus 4952*.

Standley in 1922 treated *P. palmeri* Rydb. as a synonym of *P. madrensis* Hemsl. Palmer's collection, with its lanceolate leaves, is very different from *Seemann 2167*, the type of *P. madrensis* Hemsl., which has ovate leaves densely white-pubescent with erect villose hairs.

56. **Philadelphus maculatus** (Hitchc.) comb. nov.

Philadelphus microphyllus ssp. *maculatus* Hitchc. in Madroño **7**: 44. 1943.

TYPE: *Stanford, Retherford & Northcraft 695* (in University of Washington).

Shrub with slender branchlets, the second year's growth striate, the bark light brown, strigose-pilose, hardly exfoliating, wearing off in very small pieces; the current year's growth brown, strigose-pilose, the flowering shoots with 2 or 3 pairs of leaves, the axillary buds enclosed. Leaves lanceolate or elliptic-lanceolate, 1.5–2.5 cm. long, 3–6 mm. wide, acute or obtuse at the base, acute and mucronate at the apex, uniformly strigose above, weakly sparse-strigose beneath, the hairs denser on the principal nerves, the petioles 2–2.5 mm. long, more or less dorso-ventrally flattened. Flowers solitary, the pedicels 3–4 mm. long, incanous, the hypanthium obconic, 4-ridged, with the calyx dried purplish, sparsely but uniformly strigose-pilose; sepals ovate, 5–7 mm. long, 4 mm. wide at the base, the apex acuminate, the acumen up to 2 mm. long; corolla subcampanulate, ca. 3 cm. in diameter, the petals ovate, rounded and slightly notched at the apex, white and purple-spotted at the base, stamens ca. 40, the filaments more or less united; disc glabrous, the style 1–2 mm. long, sparsely strigose at the base, the stigmata 2 mm. long, columnar, 4-ridged, the receptive surfaces linear, abaxial. Capsules subglobose, ca. 7 mm. in diameter, the persistent calyx circumferential. Seed short-caudate, the embryo 1.25 mm. long, the tail ca. one-third as long, the testa dark brown.

UNITED STATES: Arizona: Mt. Kellogg, Santa Catalina Mts., *A. Rehder 470* (A).

MEXICO: Tamaulipas: Miquihuana, *Stanford, Retherford & Northcraft 690* (MO, NY, ISOTYPE). Nuevo Leon: Sierra Madre Oriental, Galeana, *C. H. & M. T. Mueller 876* (A); *C. H. Mueller 2213* (A, MO).

This distinct and interesting species occurs on the mountain-top southwest of Miquihuana. According to the collectors it is fairly abundant among the low vegetation in the forest of large pines. Its white and purple-centered flowers appear in early August. *Rehder 470* from Arizona is a fruiting specimen. The pubescent style is very distinct. This specimen belongs here.

Hitchcock, the author of this taxon, interpreted it as a subspecies of *P. microphyllus* Gray and established its affinity with subsp. *argenteus* (Rydb.) Hitchcock. It is true that the current year's growth of this peculiar plant does have the enlarged nodes of the *P. microphyllus* type, and its hypanthium and calyx have straight appressed hairs like those of *P. argenteus* Rydb. But its four-ridged hypanthium also suggests relationship with *P. mexicanus* Schlecht., its columnar stigmata indicate affinity with *P. hirsutus* Nutt., and its pubescent style demonstrates kinship with *P. coulteri* Wats. It is probably an interspecific hybrid with the influences of all the above-mentioned species.

One of the most beautiful garden forms of *Philadelphus* at the Arnold Arboretum is the purple-heart *P.* "Bicolore," a segregate of *P.* × *purpureomaculatus* Lemoine. Recently Janaki Ammal made a study of the chromosome numbers of various cultivated *Philadelphus* species and found that "Bicolore" and a couple of its related forms have triploid chromosome numbers, 3n = 39. She credited this triploid condition to human effort

involved in the cultivation and hybridization of the widely separated geographical races and concluded that "for the first time since Eocene times polyploidy has been induced in a genus which has remained diploid for millions of years in nature." An investigation into the chromosome set-up of this natural hybrid may change the above conclusion.

The purple-centered *Philadelphus* of northeastern Mexico was introduced in Ireland in the early part of the nineteenth century by some Irish miner and has been cultivated there under the garden name "Rose Syringa." Although the plant appears to be common in Tamaulipas, representatives of the native population have never been preserved in any herbarium until Stanford, Retherford and Northcraft made their collections. Unfortunately, due to the lack of specimens for comparison, the "Rose Syringa" of the Irish gardens had been misinterpreted by Nicholson & Burbidge as *P. coulteri* Wats. The latter species has white flowers and exposed axillary buds. The oldest herbarium specimen of the cultivated purple-centered *Philadelphus* that I have examined is dated June 6, 1905. It was collected at the Botanischer Garten de Forstakadamie Muenden, Hannover. This specimen definitely has enclosed axillary buds, like *P. maculatus*. This morphological character leads me to assume that *P. maculatus* is the progenitor of, or is closely related to, the ancestors of our purple-centered triploid garden form.

The connate filaments and the lanceolate leaves of this species establish its real affinity with *P. palmeri* Rydb. The latter species can be distinguished by its densely incanous pubescence on the hypanthium and the lower surface of the leaves, and also by its glabrous style.

57. **Philadelphus stramineus** Rydb. in N. Am. Fl. 22: 172. 1905.

Philadelphus microphyllus sensu Jepson, Fl. Calif. 2: 140. 1936, pro parte, non Gray.

Philadelphus serpyllifolius sensu Fawcett, Fl. Rivers. Co. 62, 1938. — Sensu McMinn, Ill. Man. Calif. Shrubs 137, *fig. 134*. 1929, pro parte. — Sensu Abrams, Ill. Fl. Pac. St. 2: 385, *fig. 2306*. 1944, pro parte, non Gray.

Philadelphus microphyllus ssp. *stramineus* (Rydb.) Hitchc. in Madroño 7: 47. 1944. — Kearn. & Peebles, Ariz. Fl. 366. 1951. — Clokey in Univ. Calif. Publ. Bot. 24: 109. 1951, pro parte.

TYPE: California, Mono Co., White Mts., *W. H. Shockley*, Aug. 1888 (NY).

A low shrub, the branchlets fibrously striate, ash gray or straw color, the second year's growth shiny castaneous, exfoliate, the current year's growth incanous, the axillary buds enclosed. Leaves ovate-lanceolate or ovate-oblong, 10–18 mm. long, 5–8 mm. wide, obtuse at both ends, olivaceous when dry, uniformly hirsute-hispid, with a mixture of appressed and erect hairs above, strigose-pilose beneath, the hairs all appressed, the petioles 1 mm. long, dorso-ventrally compressed, incanous. Flowers solitary, rarely ternate, the pedicels 2–3 mm. long, often with 2 basal linear bracts about 5 mm. long, 1 mm. wide; hypanthium and calyx incanous, the

hairs more commonly straight, less crisp, all appressed, the hypanthium subcampanulate, 3 mm. long, 4 mm. in diameter, the sepals ovate, 5–6 mm. long, 3 mm. wide at the base, the apex acuminate; corolla disciform, 15–18 mm. across, the petals ovate, 7–9 mm. long, 5–6 mm. wide, with a few hairs at the base on the back; stamens ca. 30, the filaments distinct; disc pubescent, the style 2.5 mm. long, the stigmata 3 mm. long, separated. Capsules ellipsoid, 7 mm. long, 6 mm. in diameter, the persistent calyx supermedian. Seeds short-tailed.

UNITED STATES: **California:** Mono Co., White Mts., *W. H. Shockley*, Aug. 1888 (NY, TYPE; A, F, US ISOTYPES); *B. Maguire & A. H. Holmgren 26038* (MO); Riverside Co., San Jacinto Mts., *E. C. Jaeger*, Aug. 16, 1922 (A, US). **Nevada:** Esmeralda Co., Goldfield, *A. A. Heller 10406* (A).

This taxon is morphologically and geographically intermediate between *P. pumilus* Rydb. and *P. argenteus* Rydb. The hispid upper surfaces of the leaves of this species suggest closer relationship with the former species. At first I interpreted it as a large-leaved variety of *P. pumilus*. But a careful examination of the type collection reveals that the flowers have pubescent discs. For that reason Rydberg's original specific status is kept here.

58. **Philadelphus pumilus** Rydb. in N. Am. Fl. **22**: 173. 1905.

Philadelphus serpyllifolius sensu Hall in Univ. Calif. Publ. Bot. **1**: 83. 1902. — Sensu Munz, Man. S. Calif. Bot. 220. 1935. — Sensu McMinn, Ill. Man. Cal. Shrubs 137. 1939, pro parte. — Sensu Abrams, Ill. Fl. Pac. St. **2**: 385, *fig. 2306*, 1944, pro parte, non Gray.

Philadelphus microphyllus sensu Jepson, Fl. Calif. **2**: 140. 1936, pro parte, non Gray.

Philadelphus microphyllus ssp. *pumilus* (Rydb.) Hitchc. in Madroño **7**: 49. 1943.

TYPE: Southern California, San Jacinto Mountains, *H. M. Hall 2500* (NY).

A low, subspinescent shrub with fibrous striate gray branchlets, the second year's growth light brown, the bark closed, minutely pilose, the current year's growth brown, weakly villose, the hairs white, the axillary buds enclosed. Leaves oblong-elliptic, 5–10 mm. long, 2–5 mm. wide, obtuse at both ends, uniformly dense-hirsute with erect hairs mixed with a few longer appressed ones above, incanous with appressed straight strigose hairs mixed with some weak crisp ones beneath, the petioles 1–2 mm. long, dorso-ventrally compressed, incanous. Flowers solitary, the pedicels 1–1.5 mm. long, with the hypanthium and calyx incanous; hypanthium hemispherical, 2 mm. long, 3 mm. in diameter, the sepals ovate, 5 mm. long, 2.5 mm. wide at the base, acuminate at the apex; corolla cruciform, 14–20 mm. across, the petals oblong, 6–8 mm. long, 5 mm. wide, slightly hirsute at the base on the back, slightly notched at the apex; stamens ca. 45, the filament free; disc and style glabrous, the style 1.75 mm. long, the

stigmata 2.75 mm. long, the upper half separated. Capsules subglobose, 5 mm. in diameter, the persistent calyx circumferential. Seeds short-tailed.

CALIFORNIA: San Jacinto Mts., *H. M. Hall 2500* (NY, TYPE; A, MO, US, ISOTYPES); *E. C. Jaeger 451* (US).

The status of this xerophytic *Philadelphus* species of southeastern California has never been fully understood. Hall in 1896, 1897, and 1901 made trips to the San Jacinto Mountains and, in 1902, published a flora of that area. In that article his collections numbered *800* and *2500* were interpreted as *P. serpyllifolius* Gray, and he gave a general description of the taxon based on his no. *2500*.

Hall's identification of this material was not based on careful comparison with Gray's type, and his determination was made on what he could "make out from Dr. Gray's descriptions." Unfortunately Hall's interpretation has been adopted in most of the floras or manuals of California plants published in the last two decades. The resemblance between the Californian xerophytic *Philadelphus* as represented by Hall's *2500* and Jaeger's *451* and *P. serpyllifolius* Gray is only superficial. Both taxa have dwarf habits, subspinescent twigs, small ovate-oblong or elliptic leaves, and short flowering branchlets, each of which has a solitary flower. But *P. serpyllifolius* Gray has exposed axillary buds, columnar stigmata, ecaudate seeds, and a kinky layer of tomentum under the long strigose hairs on the lower surface of the leaves, while the California plant has enclosed buds, separate stigmata, short-tailed seeds, and straight appressed hairs on the lower surface of the leaves. According to my interpretation of the genus they belong to two different subgenera. Rydberg in 1905 described *P. pumilus*, based on Hall's *2500*, but he failed to mention that Hall had interpreted it as *P. serpyllifolius* in an earlier publication.

Jepson in 1936 gave, under the name *P. microphyllus* Gray, a description which fitted the Californian xerophytic forms, and he placed *P. pumilus* Rydb. and *P. stramineus* Rydb. as synonyms of Gray's species. Apparently this arbitrary treatment is not based on critical studies of the material representing these binomials. *Philadelphus microphyllus* Gray has glabrous sepals, a glabrescent hypanthium, and leaves almost glabrous above and sparsely villose beneath, while the California material has incanous hypanthium and sepals, and its leaves are hispid above and incanous beneath. The differences between these taxa are comparable to those existing between *P. lewisii* Pursh and *P. pubescens* Loisel., and these differences warrant specific rank for the plants.

Philadelphus pumilus Rydb. represents a plant which exists under extremely xerophytic conditions. Its incanous hypanthium and calyx with straight, appressed hairs mixed with some weaker, crisp hairs, and its incanous lower leaf surfaces with hairs of the same nature as those of the hypanthium suggest a close relationship with *P. argenteus* Rydb. It can easily be distinguished from the latter species by its hispid upper leaf surfaces.

58a. **Philadelphus pumilus** var. **ovatus**, var. nov.

Frutex foliis ovatis vel suborbicularibus, 3–7 mm. longis, 2–4 mm. latis, utrinque rotundatis vel obtusis, supra dense hispidis, pilis erectis; floribus solitariis, hypanthiis calycibusque incanis; corolla cruciformi, 12 mm. diametro, petalis oblongis, 6 mm. longis, 4 mm. latis, basi exterioribus glabris, disco et stylo glabro, stylo 1.5 mm. longo, dimidio diviso, stigmatibus clavatis, 2 mm. longis; capsulis globosis, 3 mm. diametro.

CALIFORNIA: Tacquitz Cañon, *E. C. Jaeger 463* (US, TYPE; fragment A).

This variety is distinguished from typical *P. pumilus* Rydb. by its ovate or suborbicular leaves, glabrous petals, and divided styles.

59. **Philadelphus madrensis** Hemsl. in Kew Bull. 1908: 251. 1908.

Philadelphus mexicanus sensu Seemann, Bot. Voy. Herald. 294. 1856, non Schlecht.

Philadelphus microphyllus subsp. *argyrocalyx* Hitchc. in Madroño 7: 45. 1943, pro parte.

Philadelphus microphyllus subsp. *argenteus* Hitchc., op. cit. 42, pro parte.

TYPE: Mexico: Sierra Madre, Durango, *Seemann 2167* (Kew; fragment & photo, A).

An erect shrub, old branches fibrously striate, the second year's growth castaneous, the bark exfoliate, the current year's growth strigose-villose, the hairs golden brown. Leaves ovate, those on the vegetative shoots 1.5–3.5 cm. long, 1–1.5 cm. wide, those on the flowering shoots 1–1.5 cm. long, 0.5–0.7 cm. wide, obtuse, rounded or obtuse at the base, acute at the apex, hirsute and strigose-villose above, the short hirsute hairs erect, the long villose hairs sometimes appressed, densely white-villose beneath, the hairs erect and sublanate. Flowers solitary or ternate; pedicels very short, ca. 1 mm. long, incanous, the hypanthium and calyx densely white strigose-villose, sometimes sublanate, the sepals ovate, 4 mm. long, apiculate-acuminate at the apex; corolla disciform, 2 cm. in diameter, the petals ovate-suborbicular, 1 cm. long, 8 mm. wide, the apex rounded and retuse, hirtellous on the lower and median portion of the back; stamens ca. 32, 6–7 mm. long, the filaments of 3 or 4 stamens united at the base; disc and style glabrous, the style 2 mm. long, the stigma linear, ca. 2 mm. long, the upper half divided. Capsules subglobose, 5 mm. in diameter, the persistent sepals almost circumferential. Seeds short and fat, very short caudate, the embryo 1 mm. long, the tail one fifth as long, the testa nigrescent.

UNITED STATES: **Arizona:** Mt. Graham, *Peebles, Harrison & Kearney 4449* (US), *4450* (US); Pinaleno Mts., *R. A. Darrow*, Sept. 5, 1942 (MO); Chiricahua Mts., Barfoot Park, *J. C. Blumer 1291* (F, G, MO, NY, US), *1303* (MO); *H. D. Burrall 2079* (US); Rustler Park, *R. S. Ferris 9923* (A, NY). **New Mexico:** Grant Co., the Burro Mountains, *O. B. Metcalfe 173* (G, MO, NY, US);

without precise locality. *C. Wright 1101* (MO, NY); *A. H. Berkman & A. Lee 61* (G).

MEXICO: Chihuahua: Sierra Madre, between Rio Chico & Rio Caballo, *B. Barlow*, Sept. 29, 1911 (F), Sept. 30, 1911 (F; fragment A); *Colonia Juarez*, Sept. 12, 1903 (NY, US, fragment A); Durango, *Seemann 2167* (KEW, TYPE; photo & fragment, A); Salto Canyon, Babicora, *H. LeSueur*, July 23, 1937 (F, MO); Chuhuichupa, *H. LeSueur*, Sept. 4, 1936 (F, NY).

This interesting species was discovered in the Sierra Madre in northern Mexico. Its range extends to the Graham Mountains of Arizona and the Burro Mountains in New Mexico, where it occurs at altitudes of 1850–2440 meters. Flowering specimens have been collected from June to September. The dense, long villose erect hairs on the lower leaf surface and the hirsute erect hairs on the upper leaf surface of this species form a very convenient distinguishing character. Its very short caudate seeds suggest a distant relationship with *P. hirsutus* Nutt.

Some of the specimens from the Chiricahua Mountains of Arizona are not very typical of the species. There is a gradual decrease in the density of the hairs both on the lower leaf surface and on the hypanthium.

60. **Philadelphus crinitus** (Hitchc.), stat. nov.

Philadelphus microphyllus subsp. *crinitus* Hitchc. in Madroño **7**: 45. 1943.

TYPE: Texas, *E. J. Palmer 3434* (NY).

A low shrub 1–2 m. high, the branchlets brownish gray, longitudinally fibrous striate, the second year's growth castaneous, the bark closed, rarely tardily exfoliate, the current year's growth long-villose, the hairs more or less erect and sublanate. Leaves ovate or ovate-elliptic, 1–2 cm. long, 5–10 mm. wide, rounded or obtuse at the base, acute at the apex, entire, weakly villose above, moderately to densely villose or strigose-villose beneath, the hairs appressed. Flowers solitary, very rarely ternate, the pedicels 2 mm. long, long-villose; hypanthium campanulate, long-villose and sublanate, the sepals ovate, 6–8 mm. long, 3–4 mm. wide at the base, the apex acuminate, long-villose, incanous and sublanate; corolla campanulate-disciform, 1.5 cm. in diameter, the petals suborbicular, 6 mm. in diameter, both sides glabrous; stamens 48–74, the filaments free; disc and style glabrous, the style 1–1.5 mm. long, the stigmata linear, 3–4 mm. long, free at the apex. Capsules subglobose-ellipsoid, 7–9 cm. long, 6–7 mm. in diameter, the persistent calyx circumferential. Seeds short and fat, the embryo 1–1.5 mm. long, the tail about one fourth as long, the testa brown, reticulate.

UNITED STATES: **Arizona:** Santa Catalina Mts., Mt. Livermore, *L. C. Hinckley 513* (F); *Livingstone & Thornber*, May 8, 1906 (NY); *A. Rehder 244* (A); Mt. Kellogg, *A. Rehder 459* (A); *J. J. Thornber 7319* (NY). **Texas:** Jeff Davis Co., Davis Mts., Livermore Mt., *R. S. Ferris & C. D. Duncan 2529* (MO, NY); *E. J. Palmer 30860* (A), *30916* (A, MO), *31950* (A), *34347* (NY, TYPE; A, MO, US, ISOTYPES), *34364* (A, NY).

The thick white indumentum on the lower leaf surface of the above-cited specimens resembles that of *P. madrensis* Hemsl. Yet they cannot be placed in that species because of their glabrous petals, distinct filaments, and appressed hairs on the upper leaf surface. In *P. madrensis* the petals are pubescent on the back, the filaments of two, three, or four stamens unite into small bundles, and the hairs on the upper surface are erect. This species is also closely allied to *P. argyrocalyx*, but the leaves of the latter species are only sparsely villose.

Subgenus III. **Macrothyrsus**, subg. nov.

Philadelphus subg. III. **Macrothyrsus**, subg. nov.

Philadelphus Reihe 3. *Decorticatae cymosae* Koehne, Deutsche Dendr. 181. 1863, pro parte.

TYPE SPECIES: *P. californicus* Benth.

Flores paniculatae, hypanthiis plerumque glabris, corolla cruciformi, staminibus 25–37; ovario inferiore, stigmatibus liberis, clavatis; capsulis ellipsoideis, calycibus persistentibus subapicalibus, seminibus breviter caudatis.

Frutices erecti, ramulis castaneis, corticibus exfoliatis, gemmis axillaribus expositis.

This subgenus is closely allied to the section Stenostigma of the subgenus Euphiladelphus. In fact, the type species of this subgenus, *P. californicus*, has been interpreted by many botanists as a variety of *P. lewisii* Pursh., a species of the section Stenostigma. The general appearance of these species is similar. But there are some essential differences between them which warrant placing *P. californicus* and its related species in a higher order. The first and most obvious character is the paniculate inflorescences, and the second but more fundamental one is the exposed axillary bud. In this respect the species of this subgenus show a strong trait which they have in common with the subgenera Deutzioides and Gemmatus.

Geographically, species of this subgenus are confined to the western flank of the northern and central portion of the Sierra Nevada in California. The northern end of this range overlaps with the southern periphery of the area of distribution of *P. lewisii*. As shown in Map 4, that species is concentrated chiefly in the area of the volcanic cones of the Coast Ranges in northwestern California, while species of this subgenus are found in deep ravines on the western side of the Sierra Nevada.

Section 6. **Californicus** Rydb., emend.

Philadelphus subg. III. **Macrothyrsus** sect. 6. **Californicus** (Rydb.), stat. nov.

Philadelphus Californici Rydb. in N. Am. Fl. **22**: 162. 1905, in clavi, s. stat.

Philadelphus sect. *Poecilostigma* subsect. *Paniculati* Koehne in Gartenfl. **45**: 451, 507. 1896; et in Mitt. Deutsch. Dendr. Ges. **1904** (13): 81. 1904, pro parte.

TYPE SPECIES: *P. californicus* Benth.

Character of the section as the subgenus.

KEY TO THE SPECIES

A. Hypanthium and the exterior of the sepals glabrous; lower surface of the leaves on the flowering twigs glabrous; bark of the second year's growth castaneous, usually exfoliate.
B. Panicles composed of 3-, rarely 5-flowered simple cymes ..... 61. *P. californicus.*
BB. Panicles trichotomously decompound ..... 62. *P. cordifolius.*
AA. Hypanthium and the exterior of the sepals pubescent, the lower surface of the leaves on the flowering branches hirsute, rarely glabrous; bark of the second year's growth gray and closed, rarely brown and exfoliate. 63. *P. insignis.*

61. **Philadelphus californicus** Benth. in Pl. Hartw. 309. 1849. — Walp., Ann. **2**: 614. 1851 — Torrey in U. S. Rep. Explor. Surv. Miss. Riv. Pacif. Oc. **4**: 90. 1856. — Koehne, Deutsche Dendr. 181. 1893; Gartenfl. **45**: 507. 1896, **52**: 150. 1903; et Mitt. Deutsch. Dendr. Ges. **1904** (13): 81. 1904. — Rydb. in N. Am. Fl. **22**: 164. 1905. — Schneider, Ill. Handb. Laubh. **1**: 362, *fig. 234a, a*^{2}, *236a*. 1905. — Armstrong, Field Book West. Wild Fl. 209. 1915. — Rehder, Man. Cult. Trees Shrubs 272. 1927; ed. 2, 266. 1940; et Bibl. Cult. Trees Shrubs 191. 1949. — Abrams, Ill. Fl. Pac. St. **2**: 385, *fig. 2305*. 1944. — Bean, Trees Shrubs ed. 7, **2**: 411. 1950; et in Chitt., Dict. Gard. **3**: 1546. 1951.

Philadelphus lewisii var. *parvifolius* Torrey in U. S. Rep. Explor. Surv. Miss. Riv. Pacif. Oc. **4**: 90. 1856.

Philadelphus lewisii var. *californicus* (Benth.) Gray in Bot. Calif. **1**: 202. 1876. — Hall & Hall, Yosemite Fl. 121. 1912. — Jepson, Fl. W. Mid. Cal. ed. 2, 210. 1911; Man. Fl. Pl. Calif. 465, *fig. 460*. 1925; et Fl. Cal. 2 (2): 139. 1936. — McMinn, Ill. Man. Calif. Shrubs 137, *fig. 135*. 1939.

Philadelphus fremontii Rydb. in N. Am. Fl. **22**: 165. 1905.

Philadelphus lucidus Hort. ex Lavallée, Arb. Segrez, Enum. 115. 1877.

Philadelphus gordonianus var. *californicus* Koch, Dendr. 344. 1869.

Philadelphus lewisii sensu Dippel, Handb. Laubh. **3**: 344, *fig. 181*. 1893.

TYPE: California, mountains of the Sacramento, *Hartwig 1723* (Kew; ISOTYPES G, NY).

Erect shrubs up to 3 m. high, the bark of the second year's growth castaneous, exfoliate, the current year's growth glabrous. Leaves ovate or ovate-elliptic, those on the vegetative shoots 4.5–8 cm. long, 3–5 cm. wide; those on the flowering branches 3–5 cm. long, 2–3 cm. wide, rarely up to

8 cm. long, 4.5 cm. wide, glabrous on both surfaces, sometimes barbate in the nerve angles beneath, obtuse, acute, rarely rounded at the base, 3- or 5-nerved, acute at the apex, entire, ciliate or faintly serrate. Inflorescences paniculate, lateral cymes 3-, very rarely 5-flowered, the pedicels 3–15 mm. long, the bracts linear, 3–10 mm. long, ciliate, caducous; pedicels 4–5 mm. long, glabrous; hypanthium campanulate, glabrous; sepals ovate, 4 mm. long, 3 mm. at the base, glabrous; corolla cruciform, 2.5 cm. across, the petals oblong, 11 mm. long, 5 mm. wide, glabrous on both surfaces; stamens 25–37, the anthers oblong, mucronate at the apex; disc and style glabrous. the style 4 mm. long, undivided or sometimes slightly divided; stigmata clavate or oar-shaped, the adaxial surface equal to that of the abaxial one. Capsules ellipsoid, acute at both ends, 6 -7 mm. long, 4–5 mm. in diameter, the persistent sepals supermedian, the seed ellipsoid and dorso-ventrally compressed, 1–1.5 mm. long, 0.5 mm. wide, the tail one fourth as long, the testa light brown.

UNITED STATES: **California:** Amador Co., Ione, *E. Brauton 1124* (MO, NY, US); Mokelumne Hill, *R. S. Ferris 9851* (NY); Drytown, *G. Hansen 226* (A, MO, NY); Butte Co., Chico, *A. Gray*, May 1885 (G); *A. A. Heller 11875* (F, G, US); *E. Palmer 2057* (US); *C. C. Bruce 1785* (NY), *2057* (NY); Oroville, *L. S. Rose 46423* (G, MO); Little Chico, *R. M. Austin 1785* (NY, US); Magnolia, *L. Krautter*, June 2, 1905 (G); Calaveras Co., Calaveras Range Station, Stanislaus Forest, *W. W. Eggleston 9445* (US); Humboldt Co., Alder Point, *A. Eastwood & J. T. Howell 4739* (A); Mariposa Co., El Portal, *F. R. Fosberg* (G); Mendocino Co., *H. N. Bolander* in 1867 (US); *L. R. Abrams 5959* (NY); Placer Co., Dutch Flat, *F. A. MacFadden 12838* (NY); Colfax, *M. E. Jones 3586* (A, NY, US); Shasta Co., McCloud River, *H. M. Evans*, May 30, 1924 (F); Redding, *A. A. Heller 7957* (A, F, G, MO, NY, US); Pitt, *A. Eastwood 1417* (G, US), *1417a* (US); Pitt River, *L. E. Smith 317* (A); Ingot, *A. Eastwood 7887* (A); Montgomery Creek, *A. Eastwood 652* (G, US); Tehama Co., Mill Creek, *W. W. Eggleston 7351* (NY); Tulare Co., South Fork, Kaweah River, *Culbertson 4481* (F, G, MO, NY); Middle Fork, Kaweah River, *C. S. Sargent*, Sept. 20, 1896 (A); Yuba Co., Feather River, *L. S. Rose 39237* (NY, US); Tuolumne Co., Iron Canyon, *W. J. Williamson 168* (NY); Yosemite Valley, *LeRoy Abrams 4649* (A, G, NY); Herb. L. H. Bailey *347* (BH); *H. N. Bolander 4890* (US); *W. M. Canby*, Aug. 14, 1895 (A); *H. M. Hall 9111* (US); *H. M. Hall & E. B. Babcock 3304* (NY, US); *C. C. Parry*, June 1881 (MO); *H. M. Evans*, Aug. 3, 1912 (F); Sequoia Park, *W. L. Jepson 4656* (A); locality not definite, Upper Sacramento, *W. L. Jepson*, in 1894 (US); North Fork of the American River, Fremont *511* (NY, TYPE of *P. fremontii*, MO, ISOTYPE); Sierra Nevada, *John Muir 4349* (NY); mountains of the Sacramento, *Hartwig 1723* (G, NY, ISOTYPE); without precise locality, *R. M. Austin* (F); *H. N. Bolander* in 1866 (MO); *T. Bridge 124* (A, NY, US), *125* (G, NY, US); *C. A. Purpus 5582* (A, MO, US).

CULTIVATED: Europe: Kew, *G. Nicholson*, Sept. 28, 1882 (A); *Macklean 421* (A); Hort. Bot. Berol., *E. Koehne 465* (A, MO); *A. Rehder*, July 29, 1911 (A); Bot. Garten Forstakadamie no. *40*, *H. Zabel*, July 20, 1894 (A); Hort. Bot. Haun., Sept. 1936 (A); Hort. Münden, *A. Rehder 2252* (A); Hort. Plantière, *C. K. Schneider*, June 26, 1906 (A). United States: Rochester, Highland Park no. *3*, *Wm. L. G. Edson*, July 3, 1918 (A); *Mrs. R. E. Horsey*, July 5, 1918 (BH), Sept. 21, 1917 (BH).

The type was collected from the mountains along the Sacramento River, about fifty miles south of Chico. Additional material has extended its range to Shasta County in the north and Tulare County in the south. Its altitudinal range varies from 350 to 2440 meters. It is found abundantly in moist places in the *Quercus douglasii* belt associated with *Calycanthus* and *Toxicodendron*.

This species was introduced into European gardens in 1858. It is rarely found in American gardens.

62. **Philadelphus cordifolius** Lange, Forteg. Veter.-Landboh. Frilandstr. 66. 1871; et in Bot. Tidsskr. III. **2**: 132, *pl. 3*. 1878. — Koehne, Deutsche Dendr. 181. 1893; in Gartenfl. **45**: 507. 1896; et in Mitt. Deutsch. Dendr. Ges. **1904** (13): 81. 1904. — Rydb. in N. Am. Fl. **22**: 164. 1905. — Schneider, Ill. Handb. Laubh. 366, *fig. 234, l–p, 236, f.* 1905. — Rehder, Man. Cult. Trees Shrubs 272. 1927; ed. 2, 266. 1940; et Bibl. Cult. Trees Shrubs 191. 1949.

Philadelphus lewisii var. *cordifolius* (Lange) Dippel. Handb. Laubh. **3**: 344. 1893.

LECTOTYPE: *A. A. Heller 10784* (A).

An erect shrub about 2 m. high, the basal branches up to 5 cm. in diameter, the second year's growth reddish brown or gray, 5–7 mm. in diameter, the bark exfoliate, the current year's growth glabrous. Leaves ovate, 4–10 cm. long, 3–6 cm. wide, rarely smaller, both sides glabrous, occasionally very weakly barbate in the nerve angles beneath, entire, rounded or subcordate at the base, 3- or 5-nerved, acute or rarely shortly acuminate at the apex. Flowers in compound panicles, the lateral branches 7- or 9-flowered, the peduncles 10–20 mm. long, the rachillae 4–20 mm. long, the bracts lanceolate or linear, ciliate, caducous at anthesis, pedicels 2–4 mm. long, glabrous; hypanthium campanulate, glabrous, the sepals ovate, 6 mm. long, 3 mm. wide, the apex acuminate; corolla cruciform 3–3.5 cm. across, the petals obovate-oblong, 9–17 mm. long, 6–8 mm. wide, the apex rounded, both sides glabrous; stamens ca. 27; disc and style glabrous, the style 4 mm. long, the stigmata on 4 ridges, 3 mm. long, the apical half divided. Capsules small, ellipsoid, 5 mm. long, 5 mm. in diameter at the middle, pointed at both ends, the persistent sepals supermedianly attached. Seeds very small, the embryo subglobose to ellipsoid, 0.5–0.75 mm. long, the tail one fourth to one half as long, the testa brown or castaneous.

CALIFORNIA: Amador Co., *C. B. Wolf & B. D. Stark 5474* (G); *C. B. Wolf 5128* (A, BH); Butte Co., Oroville, *A. A. Heller 10784* (A, LECTOTYPE; F, G, MO, NY, US); Chico, *Mrs. J. Bidwell*, July 1878 (G); Calaveras Co., *G. Hansen 1803* (US); Mariposa Co., *F. R. Fosberg 55036* (NY); Tuolumne Co., Mother, *H. L. Mason 2127* (G); Stanislaus Canyon, *R. Stinchfield 123* (NY); *G. G. Coning*, June 10, 1884 (G); Yosemite Valley, *H. N. Bolander 4890* (G); *H. V. Edwards*, July 1872 (NY); without precise locality, *V. Rattan 247* (US).

Philadelphus cordifolius was established on the basis of a cultivated plant of American origin. *A. A. Heller 10784* matches Lange's illustration and description and is selected as the lectotype.

Lange of Copenhagen in 1871 published *P. cordifolius* and in 1878 prepared a colored plate to illustrate the species, which he established on the strength of its large cordate-ovate leaves, up to 6.5 cm. long, and its large panicles with as many as thirty flowers. Rehder accepted this species in his last publication on the cultivated trees and shrubs. In the material of *Philadelphus* collected from California, the material cited above matches Lange's illustrations. The stems of these specimens are more robust, the leaves are larger, and the flowers are more profuse than those of the typical *P. californicus*. I suspect that they were collected from more vigorously growing plants of *P. californicus*. Lacking a field knowledge of this species, I hesitate to place Lange's species in the synonymy of *P. californicus*. This problem awaits the attention of Californian taxonomists.

I have not seen any cultivated material that can be named *P. cordifolius*. The plant labeled as such in the Arnold Arboretum does not belong here.

63. **Philadelphus insignis** Carr. in Rev. Hort. **1870**: 40. 1870. — Koehne in Mitt. Deutsch. Dendr. Ges. **1906**: 53. 1906. — Schneider, Ill. Handb. Laubh. 1: 367, *fig. 236g*. 1905. — Rehder, Man. Cult. Trees Shrubs 272. 1927; ed. 2, 266. 1940; et Bibl. Cult. Trees Shrubs 191. 1949. — Bean, Trees Shrubs ed. 7, **2**: 415. 1950; et in Chitt. Dict. Gard. 3: 1546. 1951.

Philadelphus billiardii Koehne in Gartenfl. **45**: 508. 1896. — Schelle in Beissner in Mitt. Deutsch. Dendr. Ges. **1905** (14): 18. 1905.

LECTOTYPE: Bot. Gard. Berlin, *E. Koehne 8* (MO).

An erect shrub, the bark of the second year's growth gray, closed, rarely brown and exfoliate, the current year's growth glabrous or sparsely pilose. Leaves ovate or ovate-elliptic, 3.5–8 cm. long, 1.5–6 cm. wide, obtuse, acute or rounded at the base, acute or shortly acuminate at the apex, subentire or faintly denticulate, uniformly strigose-pilose beneath or only occasionally on the principal nerves. Inflorescences paniculate, the lateral branches 3-flowered, the peduncles 8–25 mm. long, the bracts linear, 8 mm. long, pubescent; pedicels 3–5 mm. long, strigose-pilose, hypanthium and calyx strigose-pilose, sometimes nearly glabrous, sepals ovate, 7 mm. long; corolla cruciform, 2.5–3.5 cm. across, the petals oblong-obovate, 8–16 mm. long, 7–12 mm. wide; stamens ca. 30, the disc and style glabrous, the stigmata on elevated ridges, the apical half divided. Capsules ellipsoid, 6 mm. long, pointed at both ends. Seeds short-caudate, the embryo ellipsoid, 1.75 mm. long, the tail one fourth as long, the testa brown.

UNITED STATES: **California:** Amador Co., *R. S. Ferris 9851* (A, G); Butte Co., *R. M. Austin* (US); Fresno Co., Kings River Canyon, *A. Carpenter*, June 27, 1940 (G); Nevada Co., *A. M. Carpenter* (US); Shasta Co., *N. F.*

Davis 65 (NY); Tehama Co., Mill Creek, *W. W. Eggleston 7351* (US); Tuolumne Co., *W. J. Williamson 168* (US); locality not definite, near San Francisco, *A. Kellogg 247* (= 2082), June 17, 1869 (MO). **Oregon:** Washington Co., *L. Constance & A. A. Beetle 2765a* (US).

CULTIVATED: Europe: Bot. Gard. *E. Koehne 8* (MO, ISOTYPE of *P. billiardii* Koehne); Czersk, *O. Schütte 1907* (US). United States: Hort. C. S. Sargent, *A. Rehder*, June 3, 1909 (A); Highland Park, Rochester, N. Y., *Mrs. R. E. Horsey*, June 28, 1918 (BH), Sept. 4, 1918 (BH). Arnold Arboretum *543*, without collector, June 24, 1889 (A); *G. M. Merrill, 4653*, Sept. 26, 1921 (BH), June 23, 1922 (BH); without collector, June 22, 1903 (A), Oct. 3, 1916 (A).

Philadelphus insignis was established on the basis of a plant cultivated in Paris under the name "Souvenir de Billiard." Billiard was the distributor of the seed of that plant. About twenty-five years later Koehne gave the name *P. billiardii* to a plant bearing the same horticultural name. Ten years later he discovered the earlier name and made *P. billiardii* a synonym of *P. insignis*. Thus the material Koehne used as the basis for *P. billiardii* is almost true to the type of *P. insignis* Carr., and is selected as the lectotype for the species.

This species has long been regarded as a hybrid. In 1905 Schelle published a statement suggesting its parents as *P. latifolia* and *P. inodorus*. Rehder thought that it might be a hybrid of *P. pubescens* and *P. cordifolius* or *P. californicus*. The spontaneous Californian material cited above is not so uniformly pubescent as the cultivated specimens. The flowers are also smaller. Otherwise they match very well.

Subgenus IV. **Deutzioides,** subg. nov.

Philadelphus subg. IV. **Deutzioides,** subg. nov.

Philadelphus Reihe 4. *Decorticatae pauciflorae* Koehne, Deutsche Dendr. 180, 184. 1893, pro parte.

Philadelphus sect. 1. *Poecilostigma* subsect. 1. *Gemmati* Koehne in Gartenfl. **45:** 450, 486. 1896; et in Mitt. Deutsch. Dendr. Ges. **1904** (13): 77. 1904, pro parte.

TYPE SPECIES: *P. hirsutus* Nutt.

Flores solitarii vel ternati; hypanthiis turbinatis, pubescentibus vel glabris; staminibus 13 usque ad 35, ovario valide inferiore, stigmate columnare vel subcapitato, non diviso, capsulis turbinatis vel subglobosis, calycibus persistentibus apicalibus raro circumferentibus; seminibus ecaudatis.

Frutices humiles; foliis serratis vel integris, valide trinerviis; gemmis axillaribus expositis.

Species of this subgenus are exclusively North American. There are eight species in three sections. Their distribution is shown in *Maps 3* and *8*.

Section 7. **Hirsutus** Rydb., emend.

Philadelphus subg. IV. **Deutzioides** sect. 7. **Hirsutus** (Rydb.), sect. nov.

Philadelphus Hirsuti Rydb. in N. Am. Fl. **22**: 163. 1905, in clavi, s. stat.

Philadelphus sect. *Poecilostigma* Koehne subsect. *Gemmati* Koehne in Gartenfl. **45**: 450, 1896; et in Mitt. Deutsch. Dendr. Ges. **1904** (13): 77, 1904, pro parte.

TYPE SPECIES: *P. hirsutus* Nutt.

Frutex humilis, ramulis gracilibus, cortice exfoliato; foliis ovatis vel ovato-ellipticis, serratis raro subintegris, utrinque pubescentibus; floribus ternatis vel solitariis; hypanthiis hirsutis vel glabris, staminibus 25 usque ad 35; disco et stylo glabris, stigmate columnare; capsulis turbinatis vel subglobosis; seminibus ecaudatis.

Species of this section are concentrated in the southern portion of the Appalachian Highlands. Palmer's 1924 and 1928 collections extend the range of this section to the Ozark plateaus. The distribution of its species is shown in *Map 3*.

KEY TO THE SPECIES

A. Hypanthium more or less pubescent; leaves scabrous-hirsute above, uniformly villose beneath; corolla disciform with ovate or suborbicular petals ..... 64. *P. hirsutus.*

AA. Hypanthium glabrous; leaves strigose-pilose above, glabrous or with villose nerves or sparsely strigose beneath; corolla cruciform with oblong petals (except a small flowered var.) ..... 65. *P. sharpianus.*

64. **Philadelphus hirsutus** Nutt. Gen. N. Am. Pl. 1: 301. 1817. — P. W. Watson, Dendr. Brit. 1: *pl. 47*. 1825. — DC. Prod. 3: 206. 1828. — Sweet, Brit. Fl. Gard. 2: *pl. 119*. 1831. — Loudon, Arb. Frut. Brit. 2: 954, *figs. 678, 678a*. 1838. — Lindl. in Bot. Reg. **24**: *pl. 14*. 1839. — Torr. & Gray, Fl. N. Am. 1: 595. 1840. — Hooker in Bot. Mag. **88**: *pl. 5334*. 1862. — Anon. in Garden 40: 289. 1891. — Dippel, Handb. Laubh. 3: 345, *fig. 182*. 1893. — Nicholson, Kew Hand-list 1: 225. 1894; et ed. 2, 375. 1902. — Beadle in Small, Fl. 507. 1903; ed. 2, 507. 1913; et in Small, Man. 599. 1933. — Rydb. in N. Am. Fl. **22**: 169. 1905. — Schneider, Ill. Handb. Laubh. 1: 364, *fig. 234 c–d*^{2}, *235 a–e, 236 d*. 1905. — Tarouca, Freiland-laubgehölze 383, *fig. 350*. 1913; et 257, *fig. 306*. 1930. — Rehder, Man Cult. Trees Shrubs 280. 1927; ed. 2, 275. 1940; et Bibl. Cult. Trees Shrubs 194. 1949. — Bean, Trees Shrubs **2**: 413. 1950; et in Chitt. Dict. Gard. 3: 1546. 1951. — Gleason, Ill. Fl. **2**: 273. 1952.

Philadelphus villosus Muhl., Cat. 48. 1813, *nom. nud.* — Rafin., Aut. Bot. 148. 1840. — Loud., Arb. Frut. Brit. **2**: 954. 1838; et Hort. Brit. Suppl. **3**: 606. 1850, in syn.

Philadelphus hirsutus var. *gracilis* (Schrader) DC., Prodr. 3: 206. 1828.

Philadelphus gracilis Hort. ex DC., l.c., in syn. — Lubbock, Seedlings 1: 509, *fig. 328*. 1892.

Philadelphus trinervius Schrader, Dicc. 4. 1827; et in Linnaea 12: 399. 1838.

Philadelphus trinervius var. *gracilis* Schrader in Linnaea 12: 399. 1838.

Philadelphus pubescens Bosc. ex Torr. & Gray, Fl. N. Am. 1: 595. 1840, in syn., non Loisel. 1820.

Philadelphus godohokeri Kirchner in Petzold & Kirchner, Arb. Muscov. 202. 1864. — Koch, Dendr. 1: 346. 1869.

Philadelphus inodorus var. *hirsutus* A. Wood, Am. Bot. Flor. 116. 1870.

Deutzia godohokeri Hort. ex Nicholson, Kew Hand-list 1: 225. 1894; ed. 2, 375. 1902, in syn.

TYPE: *Nuttall 329* (duplicate in G, NY).

Low spreading shrubs with slender, slightly twisted, arching branches; the bark of the second year's growth castaneous, exfoliating; current year's growth villose, the axillary buds ovoid, acute at the apex, hirsute. Leaves ovate, ovate-elliptic or ovate-lanceolate, at the apex of vegetative branchlets 2.5–7.5 cm. long, 1–5 cm. wide, round at the base, acuminate or acute at the apex, uniformly scabrous-hirsute above, densely villose beneath with slightly curved trichomes, sharply serrate, those on the flowering twigs subentire with a few minute teeth. Flowers on very short shoots with 1 or 2 pairs of leaves, ternate or rarely 1 or 5, pedicels villose, 4–10 mm. or in cultivated specimens sometimes up to 20 mm. long, the long pedicellate one with 2 linear bracts 2–5 mm. below the hypanthium; hypanthium subcampanulate, villose; sepals deltoid, 4 mm. long, 3.5 mm. wide at the base, corolla disciform, 2.5 cm. across, the petals ovate, 1.2 cm. long, 1 cm. wide; stamens ca. 35, the longest 6.5 mm. long; style 4 mm. long, the stigma columnar, on 4 ridges of the united style, 2 mm. long, disk glabrous. Capsules turbinate or hemispherical, 5 mm. long, 5 mm. in diameter at the apical end, the persistent sepals apical, reflex. Seeds tailless, black, 1 mm. long, 0.5 mm. wide, the testa reticulate.

UNITED STATES: **North Carolina:** Buncombe Co., Bull Creek, Biltmore Herb. no. *4332d* (NY); Madison Co., Hot Springs, Biltmore Herb. no. *4332* (A, G, MO, NY, US), *4332b* (G, NY, US); French Broad River, *H. W. Ravenel* (NY); Polk Co., Columbus, *E. C. Townsend*, May 19, 1897 (CU, US); Rutherford Co., Chimney Rock, *Alexander, Everett & Pearson*, Sept. 27, 1933 (NY); same locality, Biltmore Herb. no. *4332a* (NY), *4332c* (A, G, MO, NY); mountains of North Carolina, *S. B. Buckley* (G, NY, US); *Wm. M. Canby*, Aug. 1876 (F, US); *G. R. Vasey* in 1878 (NY, US); without precise locality, *Chapman* (NY); Bernhardi Herb. (MO). **Georgia:** Dade Co., Sulphur Springs, *Pyron & McVaugh 1138* (US); Floyd Co., Rome, *Alexander, Everett & Pearson 2* (NY); *Pyron & McVaugh 2648* (US); Murray Co., Fort. Mt., *Pyron & McVaugh 2926* (US); Whitfield Co., *Cronquist 5053* (G, MO, US); *R. M. Harper 267* (G, NY, US), *274* (NY); Kenesan Mts., *Perry & Myers 885* (G, NY). **Tennessee:** French Broad River, *S. B. Buckley* (G); *Nuttall 329* (ISOTYPE, NY, G); *T. H. Kearney 721* (MO, NY, US); *Rugel* (NY); *C. S. Sargent* (A);

Knox Co., *H. M. Jennison 304* (TENN), *328* (TENN), *718* (TENN), *1880* (TENN); *S. C. Tain*, April 24, 1925 (TENN); *Frank & Sarah Woods 15395* (TENN); *F. Lamson-Scribner*, May 14, 1889 (NY); *A. Ruth 257* (US), *261* (NY), *244* (G, NY), May 1895 (CU, F, MO, NY, US), June 3, 1933 (TENN); *F. H. Norris 15398* (TENN); *A. B. Roger 50* (F); Marbledale, *H. M. Jennison 98* (TENN); *T. H. Kearney*, April 30, 1893 (F, US); Carter Co., *R. L. James 16819* (TENN); Chatan Co., *H. Eggert*, Aug. 19, 1897 (MO); Cheatham Co., *E. J. Palmer 35517* (A, F, MO, NY, US); *H. K. Svenson 4222* (G); Cocke Co., *A. J. Sharp 17915* (TENN); Franklin Co., *H. Eggert*, May 8, 1898 (MO, NY); Grainger Co., *Mary B. Wilson* (TENN); Hamilton Co., Chattanooga, *Florence Beckwith 1016* (US); Roane Co., Kingston, *Alexander, Everett & Pearson* (NY); Sevier Co., Little River, *H. M. Jennison 2203* (TENN); Unicoi Co., Nolichucky River, *Underwood, Harbison & Sharp 3249* (TENN); Unaka Springs, *Virginia Cook* (TENN); Van Buren Co., Caney Creek Falls, *E. B. Harger 7743* (G, TENN); Tennessee and Georgia border, Lookout Mt., *J. R. Churchill*, April 30, 1906 (G, TENN), May 6, 1906 (MO); Townsend, *R. K. Godfrey* (G); same locality, *J. B. Kinsey* (TENN); Coblerwood, *F. H. Sargent 94* (US). **Arkansas:** Faulkner Co., *D. Demaree 87* (MO); Van Buren Co., Shirley, *E. J. Palmer 25174* (A, MO). **Alabama:** Blount Co., *H. Eggert*, June 20, 1897 (MO); *C. Mohr*, June 26, 1895 (A), May 13, 1898 (A, US); Delkalb Co., *T. G. Harbison 55* (A), *5905* (A), May 15, 1899 (A); *Miss Loring*, May 1899 (US); Franklin Co., Russellville, *L. James 10* (MO); Jefferson Co., Birmingham, *E. J. Palmer 38939* (A, MO); Lauderdale Co., Florence, *C. Mohr*, June 2, 1892 (A), June 6, 1892 (MO, NY, US); Tuscaloosa Co., Black Warrior River, *E. J. Palmer 35391* (A, MO, NY, US); without precise locality, *S. B. Buckley 1892* (MO).

CULTIVATED: Europe: Kew, *G. Nicholson 1321* (A), *3131* (A); Lindley, July 9, 1838 (G); Hort. Bot. Cantab. *1844* (G), *1849* (G); *J. T. Rothrock* (F); *W. B. Basit 1842* (NY); Hort. Bot. Wien, *C. K. Schneider*, June 20, 1902 (A); Bot. Gart. Forstakadamie no. *7*, *H. Zabel*, June 17, 1873 (A); Hort. Münd, *A. Rehder 1600* (A); Bot. Gart. Darmstadt, *Purpus*, June 8, 1924 (A). United States: Arnold Arboretum *2213–1 = 542–1*, *A. Rehder*, *s.n.* (A); *2213–2 = 15358*, without collector, June 6, 1906 (A); *2213–3 = 15365*, without collector, June 6, 1906 (A), June 7, 1916 (A); *561–28*, *E. J. Palmer*, June 10, 1938 (A); Bot. Gard. Cambridge, *J. G. Jack*, June 9, 1902 (A).

Philadelphus hirsutus was discovered by Nuttall on the rocky banks of the French Broad River in Tennessee and was introduced into European gardens in the early nineteenth century under several garden names. The one most widely used was *P. gracilis* Hort. A. P. DeCandolle in 1828 took over this trade name and made it a variety of *P. hirsutus*. He differentiated this variety as having three-nerved leaves. Regarding the venation of this taxon, like that of all the other species of *Philadelphus*, the number of the principal nerves varies with the size of the leaves, which in turn depends largely upon the vigor of the shoot. The leaves on the strong growth of a plant are larger, the two side nerves branch near the base, and the leaves appear five-nerved, while the leaves on the weaker growth are smaller, the branching of the side nerves is less conspicuous, and the leaves appear three-nerved. Sweet, as early as 1831, interpreted the trade name *P. gracilis* Hort. as a synonym of *P. hirsutus*. His colored

plate represents the typical form of this species, and his interpretation is right.

Schrader was handicapped by not having seen any American specimen, and his concept of *P. hirsutus* was a mistaken one, due to his overemphasis on the form and dentation of the margin of the leaves, which he understood to be oblong-ovate and sharply and narrowly serrate. When he actually saw some material belonging to this American species, he described the larger plant as *P. trinervius* and a weaker one as *P. trinervius* var. *gracilis*.

Nicholson 1321 and *3131* are labeled *P. godohokeri* Hort. and *Deutzia godohokeri* Hort. They are typical *P. hirsutus* Nutt. These specimens prove that the *P. godohokeri* of authors in the late 1800's belongs here.

In American gardens *P. hirsutus* was introduced into cultivation as early as 1880, when A. Gattinger sent some seeds from Nashville to the Arnold Arboretum, cultivated as *2213–1 = 542–1*. In 1906 the Biltmore Arboretum also sent the Arnold Arboretum some cuttings which were cultivated as *2213–3 = 15365*. Palmer sent a plant from Shirley, Arkansas, to the Arnold Arboretum on April 7, 1928. This was cultivated as no. *561–28*, and marks the latest introduction of this species into gardens.

The center of distribution of this species is doubtlessly the southern Appalachian Mountain area, chiefly along the Tennessee River and its tributaries. There it grows along the limestone ledges and bluffs or in jumbled standstone-quartzite rocks. The few specimens collected on the Ozark Plateau are from the periphery of its range. Its white flowers appear from middle April to late May in the wild. In cultivation it is perfectly hardy in the climate of Boston. In the garden it forms a low compact shrub about 1.5 meters high with arching, spreading branches which tend to twist around each other. Those that touch the ground root readily. In the Arnold Arboretum collection of *Philadelphus* this species is one of the early bloomers.

The typical *P. hirsutus* has uniformly pubescent hypanthia and sepals. Specimens with glabrous sepals, and hypanthia pubescent only at the basal ends are interpreted as natural varieties of this species.

KEY TO THE VARIETIES OF *P. hirsutus*

A. Flowers 3 cm. across; fruit 6 mm. across the top. . . . . a. var. *intermedius*.
AA. Flowers 1.5–2 cm. across; fruit 3–4 mm. across the top . . b. var. *nanus*.

64a. **Philadelphus hirsutus** var. **intermedius**, var. nov.

Frutex, foliis ovatis, subintegris, serratis vel crasso-serratis, supra scabro-hirsutis, subtus aequabiliter villosis; floribus ternatis, basi hypanthiis pilosiusculis, corolla disciformi, 3 cm. diametro, petalis oblongo-suborbicularibus, 12–15 mm. longis, 10–12 mm. latis; capsulis turbinatis, 5 mm. longis, apice 6 mm. diametro.

UNITED STATES: **North Carolina:** Warm Springs, French Broad River, *J. D. Smith*, May 26, 1880 (fr. TYPE, US); "mountains of Georgia," *A. W. Chap-*

man 877 (F, US). **Tennessee:** Bledsoe Co., *H. K. Svenson 10175* (MO, TENN); Franklin Co., *H. Eggert*, May 8, 1898 (US, NY); Knoxville, *A. Ruth*, April 1894 (US), May 1895 (NY, US); Van Buren-Bledsoe Co., Cumberland Plateau, Fall Creeks Fall Gorge, *H. H. Iltis 3206* (TENN).

The indumentum of the leaves of this taxon resembles that of *P. hirsutus* Nutt., but the density of the hairs on the hypanthium is much reduced. In this respect it demonstrates an evolutionary tendency toward *P. sharpianus* S. Y. Hu.

64b. **Philadelphus hirsutus** Nutt. var. **nanus,** var. nov.

Frutex, foliis ovatis, subintegris, supra strigoso-pilosis, subtus aequabiliter villosis, floribus 1 vel 3, basi hypanthiis pilosiusculis, corolla parva, 1.5–2 cm. diametro, petalis ovatis, 5–7 mm. longis, 5 mm. latis; capsulis turbinatis, 3–4 mm. longis et latis; seminibus oblongo-ellipsoideis, 1 mm. longis, 0.5 mm. latis, testis reticulatis, nigrescentibus.

UNITED STATES: **Tennessee:** Blount Co., Abrams Creek, *H. M. Jennison 3824* (TYPE, TENN; fragment, A); Davison Co., near Nashville, bluff on Cumberland River, *A. Gattinger* (Curtiss no. *838* US; fragment, A).

This small-flowered variety shows relationship with *P. serpyllifolius* Gray. Gattinger ex Curtiss no. *838* is a mixture of elements belonging to different categories. That in the United States National Herbarium definitely belongs here.

65. **Philadelphus sharpianus,** sp. nov.

Frutex ca. 3 m. altus, ramis cineraceis, bienniis castaneis, 1.5 mm. crassis, exfoliatis, hornotinis 1 mm. diametro, strigoso-villosis, gemmis axillaribus ovoideis, apice acutis; foliis ovatis vel ovato-ellipticis, 3–7.5 cm. longis, 1–3.5 cm. latis, basi obtusis, raro rotundatis, apice acutis vel acuminatis, supra strigoso-pilosis, subtus a nervis sparse villosis, aliter glabris, argute serratis, petiolo 2–10 mm. longo; floribus ternatis, raro 1 vel 5, pedicellis 1–2 cm. longis, villosis, bracteolis 2, pedicellis 1–2 cm. longis, villosis, bracteolis 2, linearibus, ciliatis; hypanthiis calycibusque glaberrimis, hypanthiis obovoideis, 4 mm. longis, sepalis ovatis, 4 mm. longis, basi 3 mm. latis, acuminatis, ciliatis; corolla cruciformi, 2.5–3 cm. in diametro, petalis oblongis, 1.5 cm. longis, 8–10 mm. latis; staminibus ca. 25, antheris oblongis, disco glabro, stylo 4 mm. longo, glabro, stigmate columnari, 2 mm. longo; capsulis subglobosis, 6 mm. longis, 5 mm. diametro, calycibus persistentibus apicibus, reflexis, seminibus minutis, 1.5 mm. longis, testis nigrescentibus, reticulatis.

UNITED STATES: **Tennessee:** Great Smoky National Park, mouth of Mills Creek, lower end of Abrams Creek, *A. J. Sharp 278* (fruit, TYPE, TENN; fragment, A); Anderson Co., Lake City, *Sharp & Cain 336* (flower, TYPE, TENN; fragment, A); Norris, *W. W. Varnell*, May 15, 1937 (TENN); Roane Co., bluff near Harriman, *Underwood & Sharp 2016* (TENN, fragment, A). **Arkansas:** Van Buren Co., Red River near Shirley, E. J. Palmer 24308 (A).

CULTIVATED: Arnold Arboretum no. *18346, E. J. Palmer*, Oct. 16, 1936 (A), June 6, 1938 (A).

The distribution of this glabrous species seems to be limited to a few counties in the Great Smoky Mountain area and Van Buren County in Arkansas. It grows on sandstone ledges or river bluffs as a shrub about 10 ft. high. Its white flowers appear in late April or mid-May. Obviously it is closely related to *P. hirsutus* Nutt. From the latter species it can be readily distinguished by its glabrous hypanthium and sepals, cruciform flowers and oblong petals.

In April 1924 Mr. E. J. Palmer sent to the Arnold Arboretum a living plant no. *25174*, from Shirley, Arkansas. This plant has been cultivated under the Arnold Arboretum number *18346*. It has glabrous hypanthia and sepals, and it definitely belongs here. The herbarium specimens collected by *E. J. Palmer* and deposited in the herbaria of the Arnold Arboretum and the Missouri Botanical Garden, numbered *25174*, represent the true *P. hirsutus* Nutt.

After the manuscript on this species was prepared I received from Mr. Palmer, on May 14, 1954, a portion of his unpublished notes on the trees and shrubs of North America. His interesting account of the discovery of this species is quoted as follows:

"While collecting along the Little Red River near Shirley, Arkansas, on May 28th, 1924, I came upon a *Philadelphus* growing sparingly along the sandstone ledges of the river bluffs. The plants were all small shrubs a meter or less in height and some of the slender branches were pendulous over the rocky ledges. From the habit and vegetative characters I suspected that it was *Philadelphus hirsutus* Nutt., a plant of the southern Appalachians and the piedmont regions from North Carolina and Georgia to Tennessee. Living plants were collected and herbarium specimens were made, but as the flowers had already withered, they were not in good condition for study. On March 31st, 1928, I again visited the locality on a collecting trip with Dr. D. M. Moore and Professor Delzie Demaree of the University of Arkansas. It was then too early in the season to make specimens of the Philadelphus, but additional rooted plants were sent to the Arnold Arboretum, where plants from both collections are now growing, and where they flowered freely last year.

"The plant sent in 1928 proves to be *Philadelphus hirsutus*, and this shows a considerable westward extension of its range and the first record, so far as I am aware, from Arkansas or from west of the Mississippi River, although specimens of *Philadelphus pubescens* have sometimes been confused with it.

"The first collection of 1924, although resembling *Philadelphus hirsutus* in foliage and habit and clearly related to it in such characters as the hirsute pubescence of the foliage and branchlets and the short club-like styles, differs so strikingly in other characters of the flowers that it must be regarded as distinct. . . . In typical *Philadelphus hirsutus*, as it grows here and as shown by numerous herbarium specimens and in the excellent

illustration in the Botanical Register, 1839, pl. 14, the petals are broadly ovate and about as broad as long, overlapping at the base when the flowers are fully expanded, and the calyx and ovary are covered with hirsute pubescence. In the new variety the petals are much narrower, oblong or oblong-ovate, slightly emarginate at the apex, and not meeting at the edges, and the calyx and ovary are glabrous. The flowers appear to be slightly smaller than in the typical form and the pedicels longer, up to fully two centimeters in length."

65a. **Philadelphus sharpianus** var. **parviflorus,** var. nov.

Frutex, foliis ovatis, serratis, supra sparse pilosis, subtus sparse strigoso-pilosis; floribus ternatis, raro 5, pedicellis 7–15 mm. longis, sparse pilosis, bracteis linearibus, ciliatis, hypanthiis calycibusque glabris, corolla disciformi, 1.5 cm. diametro, petalis suborbicularibus, 7 mm. diametro.

UNITED STATES: **Tennessee:** *A. Gattinger*, May 1878 (TYPE, NY; fragment, A).

The shape of the corolla of this small-flowered variety resembles that of *P. hirsutus* Nutt., but its glabrous hypanthium and the pilose upper leaf surface indicate a closer relationship with *P. sharpianus*. Thus it is treated as a variety of the latter species.

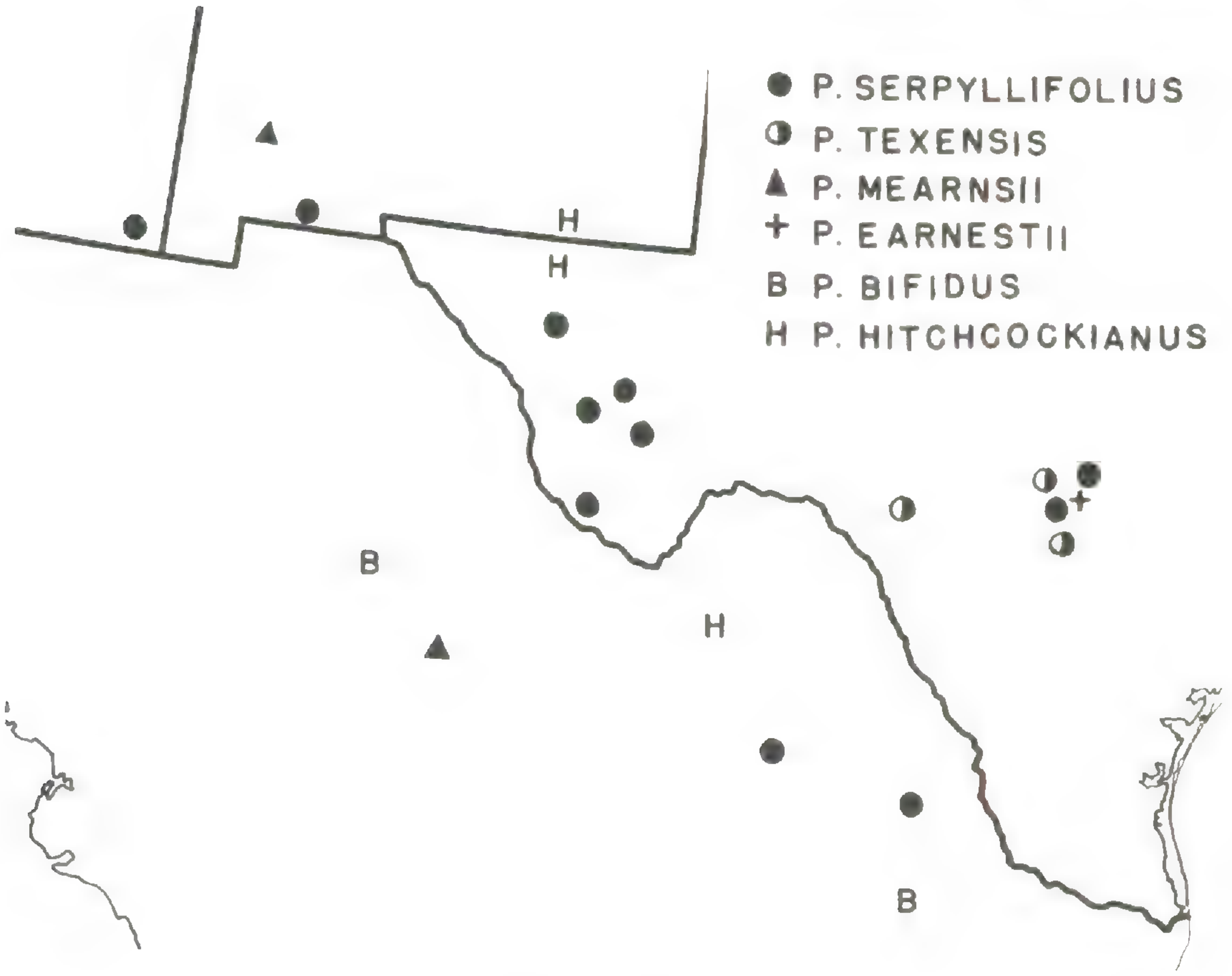
Section 8. **Pseudoserpyllifolius,** sect. nov.

Philadelphus subg. IV. **Deutzioides** sect. 8. **Pseudoserpyllifolius,** sect. nov.

Frutices humiles; ramulis floriferis brevibus; foliis parvis, integris, subtus strigosis vel strigoso-villosis, non lanatis; floribus solitaris, flore cum foliis apice calcaratis fasciculatis, pedunculis brevissimis, 1–1.5 mm. longis; hypanthiis pubescentibus vel glabris; corolla stellata vel disciformi; stylo brevissimo, 0.7–1 mm. longo, stigmate columnari; fructibus globosis vel subglobosis; seminibus ecaudatis.

TYPE SPECIES: *P. mearnsii* Evans ex Rydb.

Species in this section are xerophytic, like those in the section Serpyllifolius. They all have spinescent or calcarate branchlets, small entire leaves, solitary flowers with very short style, united stigmata, small fruits and ecaudate seeds. The principal difference between these two sections lies in the nature of the indumentum on the lower surface of the leaves. In section Serpyllifolius the lower surface of the leaves is strigose with an underlying kinky layer, while in section Pseudoserpyllifolius that kinky layer is absent. The range of this section is as shown in *Map 8*.



MAP 8. The distribution of the species of *Philadelphus* in sections Pseudoserpyllifolius and Serpyllifolius.

KEY TO THE SPECIES

A. Hypanthium pubescent; pubescence on the surface of the leaves various.
  B. Upper surface of the leaves pilose, the hairs appressed; corolla stellate or disciform; fruit 2–5 mm. in diameter.
    C. Fruit small, hemispherical, 2 mm. in diameter; corolla stellate, the petals oblong-lanceolate, 2–3 mm. wide; bark of the second year's growth castaneous, exfoliating; leaves oblong-lanceolate, 2–5 mm. wide. ..... 66. *P. mearnsii.*
    CC. Fruit subglobose, 4–5 mm. in diameter; corolla disciform, the petals suborbicular, 6–7 mm. wide; bark of the second year's growth brownish gray, not exfoliating; leaves ovate, 8–13 mm. wide. ..... 67. *P. ernestii.*
  BB. Upper surface of the leaves scabrous-hirsute, the hairs erect; corolla cruciform, the petals 5–6 mm. wide; fruit 6–7 mm. in diameter; leaves ovate or ovate-lanceolate. ..... 68. *P. bifidus.*
AA. Hypanthium glabrous; leaves strigose on both surfaces, the hairs appressed. ..... 69. *P. hitchcockiana.*

66. **Philadelphus mearnsii** Evans ex Koehne in Mitt. Deutsch. Dendr. Ges. **1904**: 79. 1904, sphalm "Mearusi," *nom. subnud.* — Rydb. in N. Am. Fl. **22**: 174. 1905, *descr.* — Standley in Contr. U. S. Nat. Herb. **23**: 310. 1922. — Tid. & Kitt., Fl. Ariz. N. Mex. 262. 1941.

Philadelphus mearnsii subsp. *typicus* Hitchc. in Madroño **7:** 54. 1943.

TYPE: *E. A. Mearns 36* (US).

Spinescent low shrub, branches gray, longitudinally rimulose, calcarate; second year's growth exfoliate, the bark reddish brown; current year's growth strigose, axillary buds subglobose (FIG. 1.), strigose. Leaves oblong-lanceolate, 5–15 mm. long, 2–5 mm. wide, cuneate at the base, acute or obtuse at the apex, strigose-pilose with appressed hairs on both surfaces, the midribs indistinct on both surfaces, the lateral ones obscure, the petioles 2 mm. long. Flowers solitary in the center of a fascicle of leaves terminating a spur; pedicels 1 mm. long, strigose; hypanthium and calyx strigose-pilose, the hairs appressed, rather uniform in size, the sepals ovate-lanceolate, 3 mm. long, 2 mm. wide, the apex caudate; corolla stellate, 2 cm. across, the petals oblong-lanceolate, 8 mm. long, 2.5 mm. wide, the apex acute or rarely notched; stamens 13–16; disk and style glabrous, the style 1 mm. long, the stigmata columnar, 1.8 mm. long. Capsule hemispherical, with flat top, the radius ca. 2 mm. Seeds ecaudate.

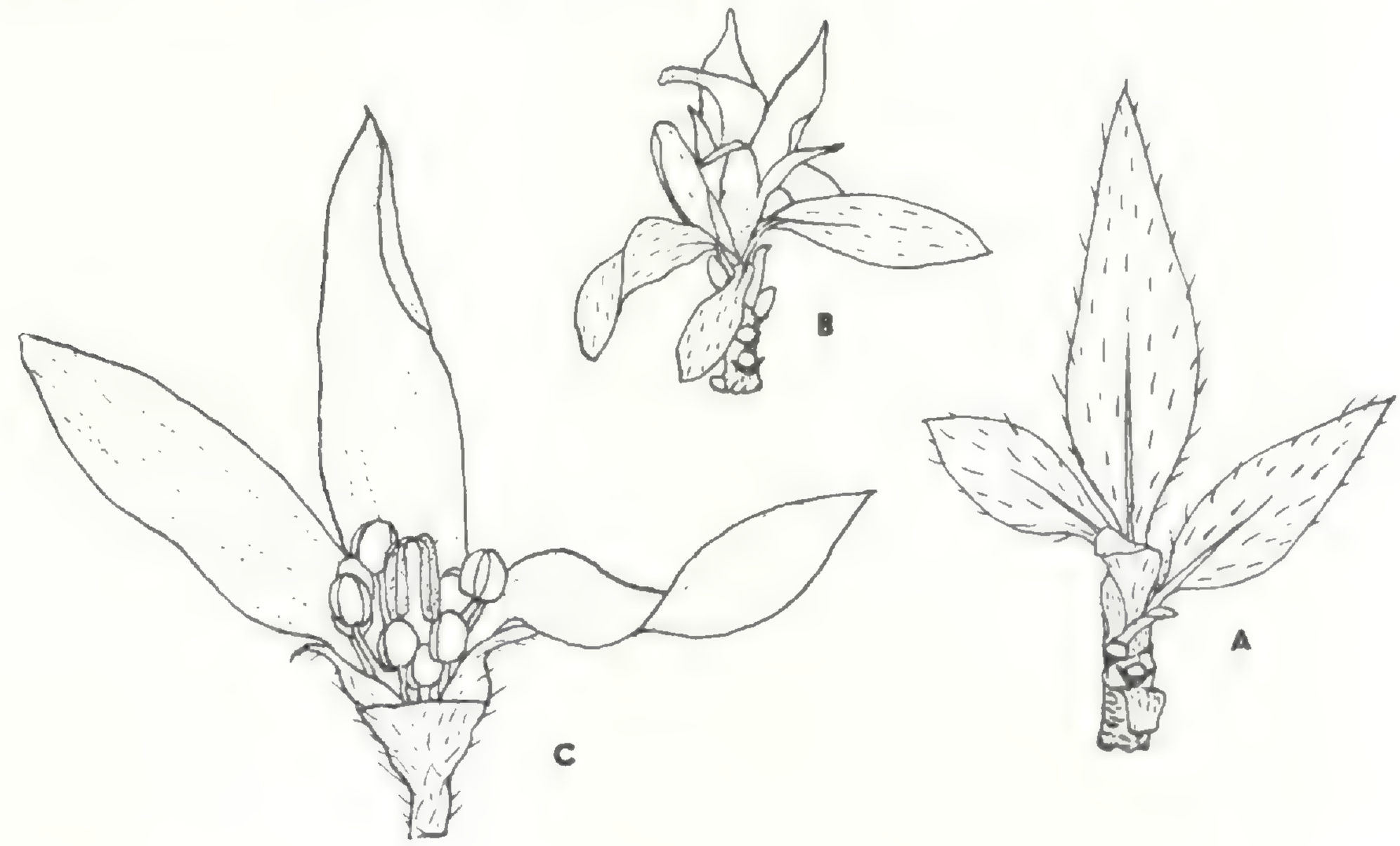


FIG. 1. *Philadelphus mearnsii* Evans (type collection, US 19135): a. An abbreviate branchlet with a terminal flower-bud and several dormant buds axillary to falling scales (× 3). b. An abbreviate branchlet with a terminal flower and several lateral axillary buds (× 3). c. A flower with one petal removed (× 5).

UNITED STATES: **New Mexico:** Grant Co., Upper Corner Monument, *E. A. Mearns 36*, May 5, 1892 (A, photo & fragment of TYPE; F, photo of TYPE; G, ISOTYPE; US, TYPE); same locality, April 28, 1892, *Mearns 36* (NY).

MEXICO: Central Coahuila, western side of Potrero de la Mula, *I. M. Johnston 9238* (A).

Dr. E. A. Mearns in the Mexican Boundary Survey collected this xero-

phytic *Philadelphus*. W. E. Evans, recognizing it as a distinct species, named it and distributed it as *P. mearnsii*. Koehne got the name from Rehder through a letter. Not knowing the validity of the publication of the binomial nor the affinity of the species, he published the name in 1904 in a discussion of *P. occidentalis* Nelson, and remarked with some doubt that they might be synonymous. This became accidentally the earliest publication of *P. mearnsii* Evans. Since it was a *nomen subnudum*, it is not accepted here. In 1905 Rydberg described the species. The material he examined was labeled *Mearns 36*, from the Upper Corner Monument, Grant Co., New Mexico. It appears that specimens so labeled were collected on different dates. As the species is credited to Evans, who was in the Smithsonian Institution, the material in that herbarium should be the type. *Philadelphus mearnsii* is a very poorly known species. Among all the specimens of *Philadelphus* that I have examined, *Johnston 9238* is the only one that matches the type.

67. **Philadelphus ernestii**, sp. nov.

Philadelphus serpyllifolius sensu Rehder, Man. Cult. Trees Shrubs 279. 1927; ed. 2, 273. 1940; et Bibl. Cult. Trees Shrubs 194. 1949. — Sensu Hitchcock in Madroño 7: 55. 1943, pro parte, non Gray.

Frutex, ramis cinereis, bienniis brunneo-griseis strigosis, 1–1.5 mm. crassis, hornotinis strigoso-villosis, gemmis axillaribus globosis; foliis ovatis, 14–28 mm. longis, 8–13 mm. latis, basi obtusis vel rotundatis, apice obtusis mucronatisque, supra sparse pilosis, subtus villosis, pilis ad basim ± crispis, petiolo 2–3 mm. longo; floribus solitariis, pedicellis 1–1.5 mm. longis, incanis; hypanthiis et calycibus sparse villosis; sepalis ovatis, acuminatis, 4 mm. longis, 2 mm. latis, corolla disciformi, 15 mm. diametro, petalis suborbiculatis, 6–7 mm. diametro; staminibus ca. 20; disco glabro, stylo 1.5 mm. longo, glabro, stigmate subcapitato-columnari, 1 mm. longo; capsulis subglobosis, 4–5 mm. diametro, calycibus persistentibus circumferentibus; seminibus ecaudatis, testis brunneis, reticulatis.

UNITED STATES: **Texas:** Kendall Co., near Boerne, Spring Creek, *Ernest J. Palmer 11595* (A, TYPE; MO), *12900* (A), *11492* (US).

Palmer 11492 is a mixture of two elements. The two sheets in the herbarium of the Arnold Arboretum are *P. texensis* S. Y. Hu, and the material in the herbarium of the United States National Museum apparently belongs here.

In the size and shape of the leaves *P. ernestii* resembles *P. texensis* S. Y. Hu. But these two species can be distinguished easily, for this species has villose hypanthia and capsules, and the lower leaf surfaces have only one kind of hairs, which are villose with the bases more or less curled. In *P. texensis* the hypanthia and fruit are glabrous, and the lower leaf surfaces have strigose appressed hairs mixed with a tight kinky covering of fine lanate tomentum.

The distribution of this species is limited to Kendall County of Texas,

where it grows on shaded rocky limestone bluffs. Its white flowers appear in mid-April, and its fruit matures in September. Mr. Ernest J. Palmer introduced this species into cultivation in 1917. The seed germinated and lived up to 1922 in the Arnold Arboretum under the field number *11313*. It was that plant which was misinterpreted as *P. serpyllifolius* by Rehder in his Manual of Cultivated Trees and Shrubs. The type material of this species has been interpreted by Hitchcock as *P. serpyllifolius* Gray. But Gray's species has pubescent hypanthia and strigose-lanate lower leaf surfaces, while the specimens cited above are strigose only.

68. **Philadelphus bifidus,** (Hitchc.) stat. nov.

Philadelphus mearnsii subsp. *bifidus* Hitchc. in Madroño **7**: 54. 1943.

Low shrub, the branchlets ash-gray, longitudinally rimulose; second year's growth castaneous, exfoliate, current year's growth villose, 1 mm. in diameter. Leaves ovate, 10–15 mm. long, 5–8 mm. wide, roundish or obtuse at the base, obtuse and mucronate, rarely acute at the apex, scabridously hirsute above, the hairs erect, rather densely strigose-villose beneath, the petioles 3–4 mm. long. Flowers solitary, the pedicel 1–2 mm. long, incanous; hypanthium and calyx sericeous, the sepals ovate, 5 mm. long, 3 mm. wide, acuminate; corolla cruciform, 15–22 mm. across, the petals oblong, 8–11 mm. long, 4–6 mm. wide, the apex bifid; stamens 24; disk and style glabrous, the style very short, 0.7 mm. long, the stigmata columnar, 1.75 mm. long. Capsules turbinate, 5 mm. long, 6 mm. across the top. Seed ecaudate.

MEXICO: Nuevo Leon: Sierra Madre near Monterey, *C. G. Pringle 13879* (G, TYPE; US). Chihuahua: *H. LeSueur 635* (F, MO, US).

This species resembles *P. mearnsii* Evans ex Rydb. in having a pubescent hypanthium. But it can be distinguished readily by its ovate leaves with scabrous-hirsute upper surface, its cruciform corolla, and its larger fruit, which measure 6–7 mm. in diameter. *Philadelphus mearnsii* has oblong-lanceolate leaves with a strigose upper surface, stellate corolla, and small fruit, which measure 2–3 mm. in diameter. Available material indicates that the distribution of this species is limited to the xerophytic mountainous area of northern Mexico.

69. **Philadelphus hitchcockianus,** sp. nov.

Philadelphus mearnsii subsp. *typicus* Hitchcock in Madroño **7**: 54. 1943, pro parte.

Frutex subspinescens, ramis cineraceis vel griseis, longitudinaliter rimulosis, bienniis cineraceis vel cineraceo-ochroleucis, hornotinis castaneis, pilosiusculis, exfoliatis, gemmis axillaribus globosis; foliis ovatis, 1–2.5 cm. longis, 6–12 mm. latis, basi obtusis, apice obtusis mucronatisque, utrinque aequabiliter brevi-strigosis, pilis appressis; petiolo ca. 2 mm. longo; floribus solitariis, pedicellis 1.5 mm. longis, strigosis; hypanthiis et

calycibus glabris; sepalis late ovatis, acuminatis, cum acumine 3 mm. longis, basi 2.5 mm. latis; corolla cruciformi, 2 cm. diametro, petalis oblongis, 8 mm. longis, 4.5 mm. latis, apice rotundatis emarginatisque; staminibus ca. 23, disco glabro, stylo 1 mm. longo, stigmate columnari, 1.5 mm. longo; capsulis turbinatis, 4 mm. longis, medio 5 mm. diametro, calycibus persistentibus subapicalibus; seminibus ecaudatis, testis brunneis, reticulatis.

UNITED STATES: **Texas:** Culberson Co., Guadalupe Mts., above McKittrick Canyon, *J. A. Moore & J. A. Steyermark 3477* (A, fr. TYPE; G, MO). **New Mexico:** Eddy Co., Carlsbad Cave, *Vernon Bailey*, May 5, 1924 (US, fl. TYPE).

MEXICO: Northern Coahuila, eastern side of the Sierra de los Guajes, Cañon de Milagro, *R. M. Steward 1728* (A).

The distribution of this species is limited to the semidesert region of western Texas and adjacent areas in New Mexico and northern Coahuila. There its white flowers appear in early May.

The first two specimens cited above were interpreted by Hitchcock as *P. mearnsii* ssp. *typicus*. The type material of *P. mearnsii* Evans has small oblong, lanceolate leaves 5–15 mm. long, 2–5 mm. wide, stellate corolla with oblong-lanceolate petals, and pubescent hypanthia and fruits. All the above-cited specimens have ovate leaves up to 25 mm. long, 12 mm. wide, cruciform corolla with oblong petals 4.5 mm. wide, and glabrous hypanthia and fruits. These differences are comparable to those existing between *P. lewisii* Pursh and *P. pubescens* Loisel., and I think a specific rank is justified.

Section 9. **Serpyllifolius**, sect. nov.

Philadelphus subg. IV. **Deutzioides** sect. 9. **Serpyllifolius**, sect. nov.

Frutices humiles; ramulis floriferis brevissimis; foliis parvis, integris, subtus strigosis lanatisque; floribus solitariis, flore cum foliis apice calcaris fasciculatis, pedicellis brevissimis, 1–1.5 mm. longis, hypanthiis pubescentibus vel glabris; corolla cruciformi, petalis oblongis; stylo brevissimo, stigmate subcapitato-columnari; fructibus turbinatis vel subglobosis; seminibus ecaudatis.

TYPE SPECIES: *Philadelphus serpyllifolius* Gray.

Species in this section are xerophytic. They are subspinescent low shrubs with very short flowering branches which appear as spurs. The trichomes on the lower leaf surfaces consist of straight strigose appressed hairs beneath which is a layer of tight kinky hairs. The styles are very short, usually only a millimeter long, and the stigmata are columnar or subcapitate clavate. The distribution of the included species is shown in *map 8*.

KEY TO THE SPECIES

A. Hypanthium villose and lanate; the upper surface of the leaves strigose with long appressed hairs and hirsute with scabridous erect ones; the persistent calyx apical on the fruit. ..... 70. *P. serpyllifolius*.
AA. Hypanthium glabrous or rarely sparsely pilose at the base; the upper surface of the leaves sparsely pilose, the hairs all appressed; the persistent calyx usually circumferential. ..... 71. *P. texensis*.

70. **Philadelphus serpyllifolius** Gray, Pl. Wright. 1: 77. 1852. — Walp., Ann. 4: 821. 1858. — Hemsl., Biol. Cent. Am. 1: 384. 1879. — Rydb. in N. Am. Fl. 22: 174. 1905. — Schneider, Ill. Handb. Laubh. 1: 364. 1905. — Standl. in Contr. U. S. Nat. Herb. 23: 310. 1922. — Metz, Fl. Bex. Co. Texas 112. 1934. — Tid. & Kitt., Fl. Ariz. New Mex. 262. 1941. — Hitchc. in Madroño 7: 55. 1943, pro parte.

TYPE: *C. Wright 1100* (Gray).

Subspinescent shrub up to 1.5 m. high; old branches cinereous, reticulately striate-sulcate, calcarate, second year's growth castaneous, exfoliate; bark strigose and sublanate, 1–1.5 mm. in diameter, buds conic, hirsute. Leaves entire, ovate, ovate-oblong, or ovate-lanceolate, 0.5–2 cm. long, 2–8 mm. wide, acute or obtuse at the base, obtuse, rarely rounded or acute at the apex, sparsely strigose and densely hirsute above, white with rather dense straight appressed hairs mixed with a close covering of very fine tangled tomentum, the petioles 2–4 mm. long. Flowers solitary, terminating the spurs, pedicels 1.5 mm. long, densely covered with straight white hairs, hypanthium and calyx incanous, the hairs more villose, appressed, and less lanate; sepals ovate, twice as long as the small hypanthium, 4 cm. long, 2.5 mm. wide, acuminate at the apex; corolla cruciform, 1–1.5 cm. across, the petals oblong, 4–6 mm. long, 3–4 mm. wide; stamens ca. 20, the filaments distinct; disk and style glabrous, the style 1.5 mm. long, the stigma columnar, 4-ridged, 1–1.5 mm. long. Capsules subglobose, 4 mm. in diameter, the persistent calyx apical. Seeds ecaudate, the testa brown, reticulate.

UNITED STATES: **Arizona:** Santa Rita Forest Reserve, *David Griffiths 4194* (US). **New Mexico:** *C. Wright 1100* (G, TYPE; MO, NY, US, ISOTYPES). **Texas:** Blanco Co., *B. C. Tharp*, May 9, 1951 (G); Brewster Co., Old Blue Glass Mts., *R. R. Innes & B. Moon 1231* (G), *1237* (G); same locality, *B. Warnock 559* (G); Trans-Pecos, *B. Warnock 866* p.p. (G); Culberson Co., *U. T. Waterfall 4529* (G, NY); Jeff Davis Co., *E. J. Palmer 30588a* (A), *34474* (A, F, MO, NY), *34508* (A); *V. L. Cory 9435* (A); *M. S. Young*, May 12, 1914 (MO, US); Kendall Co., *F. W. Pennell 10418* (NY); Presidio Co., *L. C. Hinckley 1763* (G, NY); without precise locality, *V. Havard 41* (G, US); *J. Reverchon 54* (G).

MEXICO: Rio Grande, below Donaña, Mexican Boundary Survey, *Parry, Bigelow, Wright & Schott 404* (NY, US); Coahuila, Monclova, Gloria Mts., *E. G. Marsh, Jr. 1903* (A, F), *1939* (A), *1940* (F).

The type of this species needs clarification, because the material that Gray designated as the nomenclatural type, C. Wright, n. Mexico, 1851, consists of more than one element. In the introduction of Plantae Wrightianae Gray mentioned that a full set of Wright's collection was retained in his own herbarium and another set was deposited in the herbarium of John A. Lowell, who patronized Wright's exploration. The material in the latter herbarium was transferred to the Gray Herbarium in 1941. In the Gray Herbarium there are now three sheets of the type material, all labeled in Gray's handwriting as *P. serpyllifolius* Gray. These three sheets are under two numbers, *C. Wright 1100* and *1101*, and each contains two or more elements. The sheet that was originally deposited in the Gray Herbarium is *Wright 1100*. I marked the two elements on it as (A) and (B). According to Gray's note *P. serpyllifolius* has leaves "three to five lines long and from one to two and a half wide," and the habit is "subspinescent." Element (A) fits this description well and therefore is the holotype of *P. serpyllifolius* Gray. Element (B) is *P. argyrocalyx* Wooton.

Parry, Bigelow, Wright & Schott 404 in the U. S. National Herbarium has three elements. On the lower portion of the sheet there are three individual branchlets of *P. serpyllifolius*, and on the upper portion the left-hand specimen is a *Fendlera* and the right-hand one is *Philadelphus madrensis* Hemsl. In the herbarium of the New York Botanical Garden the same number has *P. serpyllifolius* on the left and *P. madrensis* on the right.

Griffith's Arizona collection was originally labeled "*Anisacanthus thurberi* (Torr.) Gray." Hitchcock named it *P. microphyllus* ssp. *argenteus* (Rydb.) Hitchc. The lower surface of the leaves of this specimen has straight appressed hairs with a layer of silvery white kinky hairs beneath. Its branchlets also have terminal buds. Both of these characters are typical of *P. serpyllifolius* Gray.

Philadelphus serpyllifolius is a xerophytic low shrub growing along the rock banks or on the ledges of arid canyons in the southwestern corner of Arizona, southern New Mexico, and western Texas. Its closest ally is *P. texensis* S. Y. Hu. Both species are similar in appearance and their leaves are strigose and lanate beneath. *Philadelphus serpyllifolius* has a pubescent hypanthium while in *P. texensis* it is glabrous.

71. **Philadelphus texensis**, sp. nov.

Frutex ramosissimus, ramulis griseis, longitudinaliter rimulosis, biennis 1 mm. diametro, calcaratis, hornotinis ochraceis crispo-villosis, gemmis axillaribus conicis, apice acutis, pilosis; foliis ovatis, raro ellipticis, 0.6–3 cm. longis, 0.3–2 cm. latis, basi obtusis vel acutis, apice acutis, integerrimis, trinerviis, supra sparse pilosis, pilis appressis, subtus albo-villosis et lanatis, petiolo 5 mm. longo; floribus solitariis, apice calcarium sitis; pedicellis 1 mm. longis; hypanthiis calycibusque glabris, raro ad basim pilosis; sepalis deltoideis, apice acuminatis; corolla cruciformi, 1.5–2 mm. diametro, petalis oblongis, 7–8 mm. longis, 3 mm. latis; staminibus ca. 16.

basi filamentis dilatatis; disco et stylo glabris, stylo 1 mm. longo, indiviso, stigmate subcapitato-clavato; capsulis subglobosis glabris, 4 mm. diametro, calycibus persistentibus circumferentibus; seminibus ellipsoideis, 1 mm. longis, testis brunneis, reticulatis, ecaudatis.

UNITED STATES: **Texas:** Bexar Co., 30 miles north of San Antonio on Upper Classeus Ranch, on ledge of limestone bluff, *Ellen D. Schulz 115* (US, flower, TYPE; fragment, A); Edwards Co., Upper Cedar Creek, *E. J. Palmer 12333* (A, fruit, TYPE; MO, ISOTYPE); Kendall Co., Upper Cebelo Creek, *E. J. Palmer 11614* (A); Spring Creek near Boerne, *E. J. Palmer 11492* (A); Medina Co., Upper Hondo, *J. Reverchon 1523* (A, F, MO, US).

Philadelphus texensis is closely related to *P. serpyllifolius* Gray. The lower surface of the leaves of both species appears white, with straight and more or less appressed hairs beneath which is a layer of tightly kinked hairs. The corolla of both species is cruciform with oblong petals. Nevertheless the two species can be easily distinguished. In *P. serpyllifolius* the upper surface of the leaves is sparsely strigose with long appressed hairs, and uniformly densely hirsute with shorter erect ones. The calyx and hypanthium of this species are white with more straight appressed and less lanate hairs. In *P. texensis* the upper surface of the leaves is only sparsely pilose or even subglabrous with no erect hairs at all. The calyx and hypanthium of this species are definitely glabrous.

The distribution of *P. texensis* is limited to the southeastern edge of the Edward Plain of southern Texas, where it occurs on shaded limestone bluffs. Its small white flowers appear in early April.

71a. **Philadelphus texensis** var. **coryanus** var. nov.

A typo hypanthiis calycibusque aequabiliter sparse pilosis differt.

UNITED STATES: **Texas:** Bandera Co., Vanderpool, Can Creek, *V. L. Cory 49413* (A, TYPE).

This variety differs from the typical *P. texensis* in having a pilose hypanthium and calyx, the latter being apical on the fruit. In this respect it approaches *P. serpyllifolius* Gray.

HYBRIDS AND HORTICULTURAL VARIETIES

Within the last few decades many interspecific hybrids have been intentionally or accidentally produced and maintained in outstanding botanical gardens and nurseries. The parentage of some of them is known, but the pedigrees of most of them are unknown or uncertain. To facilitate their identification, a key to the hybrid species has been prepared, and in addition a general description of each hybrid species, with an annotated alphabetic list of the horticultural varieties included, is given. In the list the cultivar name is placed directly after the generic name. The important literature and specimens are also cited, so that the reader may

know the approximate time of the origin of each form and the history of its distribution.

The hybrids and horticultural varieties covered in this treatment are based on the material available on the grounds of the Arnold Arboretum and in that institution's herbarium of cultivated plants. There are a few very interesting forms, such as the first recorded tetrasomic diploid *P.* "Beauclerk," one of its parents, *P.* "Burfordiensis," and the triploid *P.* "Sybille," which are lacking from our collections. They are regretfully omitted here.

KEY TO THE HYBRID SPECIES AND ODD HORTICULTURAL FORMS

A. Flowers white, with no black eyes at center.
  B. Hypanthium glabrous.
    C. Tall shrubs 2–2.5 m. high; leaves large, those on the flowering shoots 3–11 cm. long, rarely smaller.
      D. Inflorescence compact, the pedicels of the lower flowers not elongated; flowers simple, the corolla disciform, the petals suborbicular. ..... 1. *P.* × *splendens.*
    DD. Inflorescence loose, the pedicels of the lower flowers elongated, often branched; flowers cymose.
      E. Flowers simple, the corolla stellate, the petals elliptic, acute at the apex. ..... 2. *P.* × *falconeri.*
      EE. Flowers semidoublé, double or simple, the corolla disciform or cruciform, the petals oblong or obovate, rounded at the apex. ..... 3. *P.* × *cymosus.*
    CC. Low shrubs 1–1.5 m. high; leaves small, those on the flowering shoots usually less than 3 cm. long.
      D. Flowers abundant, the corolla simple cruciform or double; the petals over 1 cm. long. ..... 4. *P.* × *lemoinei.*
    DD. Flowers few, the corolla campanulate, the petals less than 1 cm. long.
      E. Leaves ovate or ovate-oblong, 1–2 cm. wide, obtuse at both ends; bark closed. ..... 5. *P.* "Patricia."
      EE. Leaves ovate-lanceolate, 0.5–1 cm. wide, acute or rounded at the base, short-acuminate at the apex; bark exfoliate. ..... 6. *P.* "Thelma."
  BB. Hypanthium evidently pubescent.
    C. Petals oblong, obovate or suborbicular, 5 or more mm. wide.
      D. Stems nodulous; leaves glossy, pendulous, the petioles slightly twisted. ..... 7. *P.* × *pendulifolius.*
    DD. Stems normal, not nodulous; leaves not pendulous.
      E. Flowers 3 or 5, cymose or corymbose, the pedicels of the lower flowers elongated or branched.
        F. Axillary buds enclosed. ..... 8. *P.* × *polyanthus.*
        FF. Axillary buds more or less exposed. ..... 9. *P.* × *burkwoodii.*
      EE. Flowers 9, 7, rarely 5 or 3, racemose, the pedicels of the lower flowers not elongated.
        F. Flowers double or semidouble; plant 1–1.5 m. high, with stiff branches. ..... 10. *P.* × *virginalis.*

FF. Flowers simple; plant tall for the genus, the branches usually arching.
G. Extremely tall shrubs 4 or 5 m. high; stamens all sterile; no fruit observed. . . . . 11. *P.* × *maximus*.
GG. Moderately tall shrubs 2–3 m. high; stamens all fertile; fruiting freely.
H. Hypanthium and sepals scabrid-villose, the hairs dense, long, and partially erect; corolla disciform, the petals suborbicular. . . . . 12. *P.* × *nivalis*.
HH. Hypanthium and sepals strigose-pilose, the hairs short and appressed; corolla subdisciform, the petals obovate. 13. *P.* × *congestus*.
HHH. Hypanthium sparsely villose, the hairs almost erect; corolla cruciform, the petals oblong.
I. Leaves ovate; flowers 7 or 9 in loose interrupted racemes, the lower pairs of flowers in the axils of normal leaves; bark of the second year's growth gray, closed. . . . . 14. *P.* × *monstrosus*.
II. Leaves elliptic; flowers 5, 3, or 1, crowded together; bark of the second year's growth castaneous, exfoliate . . 15. *P.* "Slavinii."
CC. Petals oblanceolate, 3 mm. wide. . . . . 16. *P.* "Stenopetala."
AA. Flowers white with purplish rose or pink centers.
B. Flowers 7 in a raceme; the hypanthium and sepals glabrous. . . . . 17. *P.* "Maculiflorus."
BB. Flowers 3 or 1, rarely 5; the hypanthium sparsely or partially pilose.
C. Flowers disciform or cruciform; chromosome number diploid. . . . . 18. *P.* × *purpureo-maculatus*.
CC. Flowers subcampulate; chromosome number triploid.
D. Petals hirtellous on the inside; anthers fertile. . . . . 19. *P.* "Bicolore."
DD. Petals glabrous; anthers sterile. . . 20. *P.* "Belle étoile."

1. **Philadelphus × splendens** Rehder in Mitt. Deutsch. Dendr. Ges. 1913 (12): 158. 1913; Man. Cult. Trees Shrubs 278. 1927, ed. 2, 273. 1940; et Bibl. Cult. Trees Shrubs 194. 1949.

An upright shrub, the bark of the second year's growth castaneous, exfoliate, the current year's growth glabrous. Leaves on the flower shoots oblong-elliptic or oblong-ovate, 6–11.5 cm. long, 2.5–5 cm. wide, the base obtuse or rounded, inconspicuously remote-denticulate or subentire, the apex shortly acuminate or acute, completely glabrous or strigose-villose on the principal nerves and in their angles. Inflorescence 5-, 7-, or 9-flowered, crowded on a rachis 1.5–3 cm. long, the lower pairs in the axils of normal leaves; hypanthium and calyx glabrous, the sepals ovate, 6 mm. long, 3–4.5 mm. wide, acuminate at the apex; corolla disciform, 3.5–4 cm. across, the petals suborbicular, 1.8 mm. long, 2 mm. wide, rounded and erose at the apex; stamens 30; disc and style glabrous; stigmata oar-shaped, the adaxial surface twice as long as the abaxial.

CULTIVATED: **America:** Arnold Arboretum *6598*, *A. Rehder*, June 22, 1912 (A, TYPE); *S. Y. Hu*, June 7, 1951 (A), June 20, 1951 (A) without collector, July 2, 1917 (A); *6598-2*, *E. J. Palmer*, June 16, 1916 (A); *2–333*, *E. J. Palmer*, June 22, 1938 (A); Cambridge Botanical Garden, without collector, June 3, 1880 (A).

The origin of this hybrid is not known. Rehder suspected that its parents might have been *P. grandiflorus* and *P. gordonianus*. Its oblong-elliptic leaves, large disciform flowers, and oar-shaped stigmata resemble those of *P. inodorus* var. *grandiflorus* (Willd.) Gray, and its crowded racemose inflorescence resembles that of some garden forms of *P. coronarius*.

2. **Philadelphus × falconeri** Hort. ex Nicholson in Kew Hand-list **1**: 225. 1894, ed. 2, 375. 1902, *nom. nud.* — Sarg. in Gard. For. **8**: 494, *fig. 68*. 1895. — Möller in Deutsch. Gärtn.-Zeit. **14**: 230, *fig. 231*. 1899. — Moore in Bailey, Stand. Cycl. Hort. **5**: 2581. 1916. — Rehder, Man. Cult. Trees Shrubs 278. 1927, ed. 2, 272. 1940. — Späth, Späth-Buch 253, *fig.* 1930. — Bean in Chitt., Dict. Gard. **3**: 1546. 1951.

Bark exfoliate. Leaves ovate or ovate-elliptic, 3–6.5 cm. long, 1–2.5 cm. wide, obtuse or rounded at the base, acuminate at the apex, sparsely strigose on the primary nerves beneath, faintly denticulate. Flowers 3, 5, up to 22 in compound cymes, the peduncle of the lower pairs elongated, 2–3.5 cm. long; hypanthium glabrous; corolla stellate, the petals elliptic, acute at the apex, uniformly hirtellous on the inside; stamens sterile; style unusually long, folded in the bud. Capsules ellipsoid, the persistent sepals circumferential; seed short-caudate, 3–9 per cent fertile.

CULTIVATED: **Europe:** Hort. Späth, *C. K. Schneider* in 1902 (A); Plantière, *C. K. Schneider*, June 26, 1906 (A). **America:** Canada: Cent. Exp. Farms, Ottawa, *G. H. M. Lawrence 45* (BH); Dominion Bot. Gard., *G. H. M. Lawrence 375* (BH). United States: Arnold Arboretum *538* = 2218–1 – 15345, *Falconer*, June 18, 1877 (A, TYPE); many other collections from the type plant (A); *105–38*, *E. J. Palmer*, Sept. 29, 1940 (A).

Sargent received this plant from the Parsons Nursery, Flushing, N. Y. in 1881. Nothing was given about its origin. He suspected it of being a monstrous form of *P. coronarius*. Acute petals are found only in some forms of *P. lewisii*. The oblong-elliptic petals and the ellipsoid fruit with circumferential persistent calyx suggest a relationship with *P. lewisii*. The ovate-elliptic leaves and the true cymose inflorescence suggest a relationship with *P. inodorus*. The hirtellous petals show some influence of *P. mexicanus*. All these are New World species. No Old World elements possess the above-mentioned characters to contribute to *P. falconeri*. It must be New World in origin. This species has been distributed by Mrs. W. W. Gibbs, Staunton, Va., as *P. cordifolius* and by the Späth Nursery near Berlin as *P. insignis*.

3. **Philadelphus × cymosus** Rehder in Jour. Arnold Arb. 1: 201. 1920; Man. Cult. Trees Shrubs 279. 1927, ed. 2, 274. 1940; et Bibl. Cult. Trees Shrubs 194. 1949.

Philadelphus floribundus Schrader ex DC., Prodr. 3: 205. 1852. — Moore in Bailey, Stand. Cycl. Hort. 5: 2580. 1916. — Rehder, Man. Cult. Trees Shrubs 277. 1927, ed. 2, 272. 1940; et Bibl. Cult. Trees Shrubs 194. 1949, non Roemer & Usteri, 1790.

Erect shrubs 0.5–2.5 m. high, bark brown or castaneous, exfoliate. Leaves ovate. Flowers ternate, single, or five in cyme-like crowded racemes, the pedicels of the lower pairs of the racemes elongated, sometimes branched; hypanthium glabrous; sepals leafy, ovate-lanceolate.

Rehder included some of these forms in *P.* × *polyanthus*, which is characterized as having a pubescent hypanthium. They are transferred here because the hypanthium is glabrous.

3a. **Philadelphus** "Amalthée" Lemoine, Cat. 197: 17. 1923.

Leaves ovate-elliptic, 3–5 cm. long, 11–18 mm. wide, very sparsely strigose-pilose beneath; obtuse at the base, shortly acuminate at the apex, subentire or with 1 or 2 minute teeth on each side; corolla disciform, 3 cm. across, the base of the petals becoming pinkish at the latter part of anthesis.

CULTIVATED: Arnold Arboretum *16221*, *A. Rehder*, June 28, 1927 (A).

3b. **Philadelphus** "Bannière" Lemoine, Cat. 164: 24. 1906. — Rehder in Jour. Arnold Arb. 1: 201. 1920; et Man. Cult. Trees Shrubs 280. 1927, ed. 2, 274. 1940.

Leaves ovate, 5–7 cm. long, 2.5–4 cm. wide, rounded at the base, short-acuminate at the apex, each side 4- up to 7-serrate, glabrous and barbate in the nerve angles beneath; flowers semi-double, the anthers all sterile, some petaloid; corolla 4–4.5 cm. across, the outer petals obovate, 18 mm. long, 16 mm. wide, rounded at the apex; capsule globose; seed short-caudate, a few fertile.

CULTIVATED: Arnold Arboretum *7594* (A); Highland Park, *R. E. Horsey*, June 4, 1918 (BH), Sept. 4, 1918 (BH).

The plant was introduced from the Lemoine Nursery before 1910. It flowered in the Arnold Arboretum in 1914.

3c. **Philadelphus** "Bouquet blanc" Lemoine, Cat. 155: VII. 1903, 188: 12. 1915. — Rehder, Man. Cult. Trees Shrubs 279. 1927, ed. 2. 274. 1940.

Philadelphus "Albâtre" Lemoine, Cat. 183: 5. 1913, 188: 12. 1915.

Philadelphus × *virginalis* Rehd. "Albâtre" Rehd., Man. Cult. Trees Shrubs ed. 2. 274. 1940.

Bark grayish brown, closed; leaves small, subentire, ovate, 2–5 cm. long, 1–3 cm. wide, rounded at the base, pubescent on the nerves beneath; flowers 7 or 9, double, 2.5 cm. across, some crowded, others in a loose raceme, stamens partially fertile.

CULTIVATED: Arnold Arboretum *5089*, *A. Rehder*, July 2, 1918 (A); *E. J. Palmer*, June 11, 1936 (A), June 22, 1938 (A); Arnold Arboretum *7593*, *A. Rehder*, June 19, 1919 (A), June 30, 1920 (A).

Arnold Arboretum *5089* was introduced from the Lemoine Nursery in 1905, two years after the announcement of the production of this garden form. It represents a genuine *P.* "Bouquet blanc." Arnold Arboretum *7593* is labeled as *P.* × *virginalis* Rehd. "Albâtre." This specimen probably represents the true *P.* "Albâtre" for when Lemoine announced this form he described it as a "Plant extremely floriferous, in the group of the good variety "Virginal." In habit and the appearance of the double flowers, what Lemoine called *P.* "Albâtre" resembles *P.* × *virginalis*. But the latter hybrid is characterized by its pubescent hypanthium and *P.* "Albâtre" has glabrous ones. In the more or less closed bark, double flower and glabrous hypanthium this form is identical with *P.* "Bouquet blanc."

3d. **Philadelphus** "Campbell's seedling" Hort.

Leaves very small, ovate, 1.5–3 cm. long, 9–18 mm. wide, obtuse at the base, short-acuminate at the apex, sparsely pilose beneath, some variegated; flowers simple, 5 in crowded racemes or rarely one, corolla disciform, 3.5 cm. across, stamens all fertile, style divided to the disc, the stigmatic surface adaxial.

CULTIVATED: Arnold Arboretum *104–38–B*, *E. J. Palmer*, June 24, 1943 (A).

This is a newly developed form. The Arnold Arboretum received its cuttings from Mrs. W. W. Gibbs, Gibbs Hill, Staunton, Va., in 1933. Nothing is known about its origin.

3e. **Philadelphus** "Conquête" Lemoine, Cat. **155**: VIII. 1903, **188**: 12. 1915. — Moore in Bailey, Stand. Cycl. Hort. **5**: 2581. 1916. — Rehder in Jour. Arnold Arb. 1: 201. 1920; et Man. Cult. Trees Shrubs 280. 1927, ed. 2, 274. 1940.

A low erect shrub less than 1 m. high; leaves ovate-lanceolate, 5.5–6.5 cm. long, 2–3 cm. wide, obtuse at the base, acuminate at the apex, serrate, sparsely strigose-pilose beneath; flowers 3 or 5, sometimes 7, with the lower pair cymose; corolla cruciform, 5.5 cm. across; petals obovate, the apex rounded and erose; some anthers petaloid; style divided to the base.

CULTIVATED: Arnold Arboretum *5090* (A, BH).

Rehder designated this form as the type of the hybrid *P.* × *cymosus*.

3f. **Philadelphus** "Dresden" Moore in Bailey, Stand. Cycl. Hort. **5**: 2582. 1916.

Bark castaneous; leaves ovate-elliptic, 2.5–5.5 cm. long, 1.5–2.5 cm. wide, obtuse at the base, acuminate at the apex, with 6–10 sharp teeth on each side, glabrous except along the principal nerves beneath; flowers simple, ternate or solitary; corolla disciform, 3 cm. across, the petals suborbicular.

CULTIVATED: Arnold Arboretum *473–36, E. J. Palmer*, June 7, 1938.

This plant was introduced in 1936 from H. A. Hesse, Weener-a-d-Ems, Germany. Nothing is known about its origin.

3g. **Philadelphus** "Gladwyne" Hort. ex Wyman, Shrubs Vines Am. Gard. 422, 1949, *nom. nud.*

Bark gray, tardily exfoliate; leaves ovate, 2.5–4 cm. long, 1–3 cm. wide, rounded or obtuse at the base, acute or short-acuminate at the apex, serrate, sparsely strigose-pilose beneath; flowers semidouble, ternate or solitary, the corolla 2.5 cm. across; style divided almost to the base.

CULTIVATED: Arnold Arboretum *292–41, E. J. Palmer*, June 24, 1943.

This plant was introduced in 1941 from the Upper Bank Nursery, Media, Pa.

3h. **Philadelphus** "Mer de glace" Lemoine, Cat. **167**: VIII. 1907. **170**: 26, *t.* [5]. 1908. — Rehder in Jour. Arnold Arb. 1: 201. 1920; et Man. Cult. Trees Shrubs 280. 1927, ed. 2, 274. 1940.

Leaves ovate, 4.5–7 cm. long, 2.8–4 cm. wide, obtuse at the base, shortly acuminate at the apex, each side with 6–15 sharp teeth, sparsely strigose-pilose beneath; flowers 3, rarely 5 or 1, semidouble, the corolla 4.5 cm. across, the outer petals obovate, the apex rounded, the style divided to the base.

CULTIVATED: Arnold Arboretum *5880–1 = 1190–24, A. Rehder*, July 2, 1918 (A).

3i. **Philadelphus** "Monster" Hort.

Leaves ovate-elliptic, 5–6 cm. long, 2–2.5 cm. wide, obtuse at the base, acuminate at the apex, undulate and serrate, along the nerves villose or pilose; flowers 5, 3, or 1, not fragrant; corolla 3–3.5 cm. across; style divided almost to the base.

CULTIVATED: Arnold Arboretum, Weston Nursery, *S. Y. Hu*, June 14, 1951 (A).

3j. **Philadelphus** "Nuée blanche" Lemoine, Cat. **155**: 23. 1903. **188**: 12. 1915. — Moore in Bailey, Stand. Cycl. Hort. **5**: 2581. 1916. —

Rehder in Jour. Arnold Arb. 1: 201. 1920; et Man. Cult. Trees Shrubs 280. 1927, ed. 2, 274. 1940.

Leaves ovate, 2.5–5 cm. long, 1.5–2.5 cm. wide, obtuse or acute at the base, shortly acuminate at the apex, subentire or each side with 1 or 3 teeth, sparsely strigose-pilose beneath; flower solitary or ternate, semi-double, the corolla 2.5–3 cm. across, disciform.

CULTIVATED: Arnold Arboretum *5093*, *G. M. Merrill*, June 6, 1922 (BH); *C. E. Kobuski & C. K. Allen*, June 7, 1933 (A).

This plant was introduced from Lemoine Nursery in 1905.

3k. **Philadelphus** "Perle blanche" Lemoine, Cat. **146**: XI. 1900. — Moore in Bailey, Stand. Cycl. Hort. **5**: 2581. 1916. — Rehder in Jour. Arnold Arb. 1: 201. 1920; et Man. Cult. Trees Shrubs 280. 1927, ed. 2. 274. 1940.

Bark castaneous, closed, slowly wearing off; leaves ovate or elliptic, 4–8 cm. long, 1.5–3.2 cm. wide, obtuse or acute at the base, acuminate at the apex, entire, glabrous; flowers 5 or 7, the lower pairs in the axils of normal leaves, corolla cruciform, 3.5 cm. across, the petals obovate-oblong.

CULTIVATED: Arnold Arboretum *1050–36*, *E. J. Palmer*, June 24, 1943 (A); *S. Y. Hu*, June 12, 1951 (A).

3l. **Philadelphus** "Rosace" Lemoine, Cat. **158**: VIII. 1904, **188**: 12. 1915. — Moore in Bailey, Stand. Cycl. Hort. **5**: 2581. 1916. — Rehder in Jour. Arnold Arb. 1: 201. 1920; et Man. Cult. Trees Shrubs 280. 1927, ed. 2, 274. 1940.

Bark castaneous, closed, slowly wearing off; leaves elongate-ovate, 6.5–10 cm. long, 2.5–5 cm. wide, obtuse at the base, acuminate at the apex, sparsely pubescent beneath; flowers large, 5 in a true cyme or 3, the corolla 5 cm. across, the petals obovate, 2.5 cm. long, 2.5 cm. wide, the style divided to the base.

CULTIVATED: Arnold Arboretum *5095* (A); Highland Park, *R. E. Horsey*, June 11, 1918 (BH).

This plant shows strongly the influence of *P. inodorus*.

3m. **Philadelphus** "Velleda" Lemoine, Cat. **169**: 17. 1923.

Bark exfoliate; leaves small, ovate, 1.5–3 cm. long, 8–15 mm. wide, subentire or each side with 2–4 coarse teeth; flowers solitary, the corolla disciform, 2.5 cm. across, the petals suborbicular.

CULTIVATED: Arnold Arboretum *19269*, *E. J. Palmer*, June 11, 1936 (A).

This plant was introduced from the Lemoine Nursery in 1925. It shows strongly the influence of *P. inodorus*.

3n. **Philadelphus** "Undulatus" Petzold & Kirchner, Arb. Muscav. 205. 1864. — Koch, Dendrol. 341. 1869. — Nicholson, Kew Hand-list 1: 227. 1894, ed. 2, 377. 1902.

Bark castaneous, exfoliate; leaves ovate-elliptic, serrate, sparsely pilose beneath; flowers semidouble.

CULTIVATED: Hort. Leipzig, *C. K. Schneider*, June 26, 1901 (A).

This plant shows the influence of *P. inodorus* strongly. It is probable that it no longer exists in cultivation.

3o. **Philadelphus** "Umbellatus" Koehne, Deutsche Dendr. 183. 1893.

Philadelphus zeyheri var. *umbellatus* (Koehne) Rehder in Jour. Arnold Arb. 1: 201. 1920; et Man. Cult. Trees Shrubs 277. 1927, ed. 2. 272. 1940.

A low shrub, 1 m. high, the bark castaneous, exfoliate, the current year's growth glabrous; leaves ovate-elliptic, 6–9 cm. long, 1.5–6.5 cm. wide, obtuse at the base, acuminate at the apex, prominently denticulate, rarely subentire, sparsely pilose on both surfaces or glabrescent above; flowers 10 up to 15 in loose panicles, rarely fewer in depauperate racemes, the hypanthium and sepals glabrous; corolla disciform, 2.5–4 cm. across, the petals obovate or suborbicular, 1.2–1.8 cm. in diameter, rounded at the apex; stamens all sterile; style longer than the stamens, glabrous; capsules ellipsoid, 8 mm. long, 6 mm. in diameter.

CULTIVATED: **Europe:** Hort. Göttingen, *A. Rehder 384* (A), *402* (A), *1671* (A), July 1, 1890 (A). **United States:** Arnold Arboretum *3855*, *A. Rehder*, July 18, 1918 (A), June 19, 1919 (A); *S. Y. Hu*, June 7, 1951 (A); Bot. Gard. Cambridge, *A. Rehder*, June 7, 1918 (A); Glenn Dale Introduction Garden *PI59426*, *W. H. Cowgill 688* (BH).

This horticultural form has been cultivated in German gardens since the 1890's. Its origin is not known. The pilose leaves, exfoliate bark, disciform corolla, and elongated style suggest some relationship with the *P. inodorus* complex. The Arnold Arboretum obtained its plant from the Späth Nursery in 1908. It produces few flowers. The field note of *Cowgill 688* gives the origin of that specimen as Yunnan, China. But the specimen bears no character of the *Philadelphus* known to Yunnan. There may be a mistake in the labeling of the plant.

4. **Philadelphus** × **lemoinei** Lemoine Cat. ? 1887, **109**: 24. 1888. — Anon. in Wien. Ill. Garten-Zeit **1888**: 124. 1888. — Sargent in Gard. For. **2**: 616, *fig. 154*. 1889. — Koehne in Gartenfl. **45**: 507. 1896. — Darnell in Hardy Plants **1**: 197. 1930. — Rehder, Man. Cult. Trees Shrubs 279. 1927, ed. 2, 273. 1940. — Späth, Späth-Buch 254, *fig. 255*. 1930. — Bean in Chitt., Dict. Gard. **3**: 1546. 1951.

A compact low shrub, spreading as wide as the height of the plant; bark exfoliate; leaves ovate, 1.5–2.5 cm. long, 7–12 mm. wide, glabrous

above, sparsely strigose beneath, rounded or obtuse at the base, short-acuminate at the apex, with 2 or 3 teeth on each side; flowers ternate or solitary, rarely 5, the hypanthium glabrous, the sepals ovate, 4 mm. long; corolla cruciform, 2.5–3 cm. across, the petals ovate, erose at the apex; style 3 mm. long, divided almost to the base, stigmata 2.5 mm. long, clavate.

CULTIVATED: **Europe:** Bot. Gart. Forstakadamie *44, H. Zabel*, June 20, 1894 (A); Plantière, *C. K. Schneider*, Sept. 1903 (A); Hort. Bot. Wien, *C. K. Schneider*, June 21, 1902 (A). **United States:** Arnold Arboretum *1830*, without collector, June 30, 1890 (A); *3449*, without collector, June 27, 1904 (A); *1830–B, E. J. Palmer*, June 22, 1938 (A); Glenn Dale Introduction Garden, Maryland, *P. I. 52455, W. H. Cowgill 714* (A, BH).

In 1884 Lemoine produced this hybrid by applying the pollen of a garden form of *P. coronarius* to *P. microphyllus*. The seedling flowered when less than three years old. In 1888 it was introduced into the Arnold Arboretum. The plants numbered *P. I. 52455* are distributed as *P. tenuifolius* or *Deutzia* sp.

4a. **Philadelphus** "Avalanche" Lemoine, Cat. 132: 5. 1896. — Möller's Deutsche Gärtner-Zeit. 22: 379, *fig.* 1907. — Gard. Chron. III. 21: 89, *fig. 25.* 1897. — Rehder, Man. Cult. Trees Shrubs 279. 1927, ed. 2, 273. 1940.

An erect shrub up to 2 m. high, bark gray, closed; leaves elliptic, 2–2.5 cm. long, 5–8 mm. wide, acute at both ends, both sides glabrous, entire; flowers 7, rarely 5 or 9; corolla cruciform, 2–2.5 cm. across, the petals obovate-oblong, 10 mm. long, 8 mm. wide, rounded at the apex.

CULTIVATED: Arnold Arboretum *4154*, without collector, June 22, 1903 (A), June 29, 1906 (A).

This form shows the influence of *P. lewisii*.

4b. **Philadelphus** "Bonje" Hort.

Bark slowly wearing off; leaves very small, ovate-elliptic, those on the flowering shoot 9–14 mm. long, 4–5 mm. wide, obtuse at the base, acute at the apex, entire, sparsely pilose on the nerves beneath; flowers solitary, ternate, or very rarely five, the corolla semidouble, 1.5 cm. across.

CULTIVATED: Arnold Arboretum *734–36, E. J. Palmer*, June 22, 1938 (A).

This form was distributed by the John Siebenthaler Nurseries, Dayton, Ohio. Nothing is known about its origin.

4c. **Philadelphus** "Candélabre" Lemoine, Cat. 127: 24. 1894. — Reh-

der in Möller's Deutsch. Gärtn.-Zeit. **11**: 294. 1896; et Man. Cult. Trees Shrubs 279. 1927, ed. 2, 273. 1940.

Bark castaneous, closed, tardily exfoliate; leaves ovate, 1.5–2.3 cm. long, 6–11 mm. wide, rounded at the base, acuminate at the apex, entire, villose on the nerves beneath; flowers solitary, rarely ternate, the corolla almost cup-shaped, 3.5 cm. across becoming cruciform, the petals ovate, obtuse at the apex, erose, 13 mm. long, 11 mm. wide.

CULTIVATED: Arnold Arboretum *4151*, without collector, June 27, 1904 (A), June 25, 1909 (A).

This is one of the most beautiful garden forms. Its large flowers resemble those of *P.* "Bicolore" but do not have the purplish center. It was produced by the Lemoine Nursery in 1894 and introduced into the Arnold Arboretum before 1904.

4d. **Philadelphus** "Coupe d'argent" Lemoine, Cat. **189**: 20. 1915. — Anon. in Gard. **86**: 332, *fig.* 1922, **87**: 116, *fig.* 1923.

Bark castaneous, exfoliate; leaves ovate, 2.5–4 cm. long, 1–1.5 cm. wide, rounded at the base, acute or shortly acuminate at the apex, minutely serrate, with 2–4 teeth on each side, sparsely pilose on the primary nerves beneath; flowers ternate, rarely 5 with the lower pair in the axils of normal leaves; corolla disciform, 3 cm. across, the petals orbicular, 1.5 cm. in diameter.

CULTIVATED: Arnold Arboretum *19260*, *E. J. Palmer*, June 10, 1937 (A); *S. Y. Hu*, June 13, 1951 (A); *400–36*, *E. J. Palmer*, June 20, 1938 (A).

This form was introduced from the Lemoine Nursery in 1925. Its leaves resemble *P.* × *lemoinei*, from which it can be distinguished by its disciform flowers. It shows strongly the influence of *P. inodorus*.

4e. **Philadelphus** "Dame blanche" Lemoine, Cat. 177: 7. 1911, **188**: 12. 1915.

A very small, delicate shrub, the bark nigrescent, closed, tardily wearing off; leaves ovate, 1.5–2 cm. long, 7–8 mm. wide, obtuse or rounded at the base, acute at the apex, sparsely strigose on the primary nerves beneath; flowers 5, rarely 3, the sepals ovate, acuminate, the corolla disciform, 14–18 mm. across, the petals obovate, 8 mm. long.

CULTIVATED: Arnold Arboretum *21990*, *E. J. Palmer*, June 18, 1936 (A).

This form was introduced into the Arnold Arboretum in 1926 in the form of cuttings from the Späth Nursery. It shows the influence of *P. lewisii* strongly.

4f. **Philadelphus** "Erectus" Lemoine, Cat. 121: 23. 1892. — Rehder in Möller's Deutsche Gärtner-Zeit. 11: 294. 1896; et Man. Cult. Trees

Shrubs ed. 2. 274. 1940. — Hasach in Möller's Deutsche Gärtner-Zeit. 17 : 383. *fig.* 1902.

A very low shrub, the bark grayish or nigrescent, closed and tardily wearing off; leaves elongate-ovate to sublanceolate, 1.5–4.5 cm. long, 8–18 mm. wide, obtuse or rounded at the base, gradually elongate and acute or acuminate at the apex, serrate, with 1 or 3 teeth on the apical end of each side, at the basal end sparsely and partially pilose; flowers ternate, rarely 5 with the lower pair in the axils of normal leaves, the sepals ovate, long-acuminate, the corolla cruciform, the petals oblong.

CULTIVATED: **Europe:** Bot. Gart. Forstakadamie *46, H. Zabel*, June 20, 1894 (A); Plantière, *C. K. Schneider*, June 26, 1906 (A). **United States:** Arnold Arboretum *4152*, without collector, June 29, 1909 (A); *19–36, E. J. Palmer*, June 24, 1943 (A), Sept. 20, 1940 (A).

This form was developed by the Lemoine Nursery in 1890. It shows strongly the influence of *P. inodorus* var. *laxus*.

4g. **Philadelphus** "Innocence" Lemoine, Cat. **201**: 18. 1928.

Leaves small, ovate-lanceolate, those on the flowering shoot 2.5–3.5 cm. long, 7–15 mm. wide, acute at both ends, strigose-pilose on the nerves beneath; flowers 5 or 7, crowded on short branches, the corolla 3–3.5 cm. across, disciform, the style divided almost to the base.

CULTIVATED: Arnold Arboretum *21882 288–32, E. J. Palmer*, Aug. 18, 1936 (A), June 24, 1943 (A).

4h. Philadelphus "Manteau d'hermine" Lemoine, Cat. **140**: IX. 1898. **188**: 12. 1915. — Rehder, Man. Cult. Trees Shrubs 279. 1927; ed. 2, 274. 1940.

A depauperate low shrub, the bark grayish brown, closed; leaves yellowish green, small, ovate-elliptic, rarely ovate, 7–25 mm. long, 4–12 mm. wide, acute at both ends, pilose on the nerves beneath; flowers inodorous, double, the bud pinkish, the corolla 2.3–3 cm. across, the outer petals oblong.

CULTIVATED: **Europe:** Hort. Plantière, *C. K. Schneider*, June 26, 1926 (A). **United States:** Arnold Arboretum *4156*, without collector, June 20, 1901 (A), June 25, 1909 (A); *S. Y. Hu*, June 14, 1951 (A).

This form was produced by the Lemoine Nursery in the 1890's. Its pink flower bud shows the influence of *P. pekinensis* to some extent.

5. **Philadelphus** "Patricia" Hort. ex Wyman, Shrubs Vines Am. Gard. 422. 1949.

A low, erect, tufted shrub 1 m. high; bark of the second year's growth gray, closed, the current year's growth hirtellous; the buds enclosed. Leaves ovate or ovate-oblong, 2–4 cm. long, 1–2 cm. wide, obtuse at both

ends or acute at the apex, entire or faintly sinuate-denticulate, with 1 or 2 teeth on each side, sparsely hirsute on both surfaces. Flowers 3 or 5; the hypanthium glabrous or with a few hairs at the base; sepals ovate, 3–4 mm. long; corolla cup-shaped, the petals obovate, 10 mm. long, 6–7 mm. wide; stamens ca. 15 fertile, or poorly developed and sterile; disc and style glabrous.

CULTIVATED: Arnold Arboretum *605–39*, *E. J. Palmer*, June 24, 1943 (A). *S. Y. Hu*, June 13, 1951 (A).

This interesting little plant produces few flowers. Its dark green foliage and upright habit give it a very characteristic appearance, which is different from any other *Philadelphus* in the Arnold Arboretum collection. It reminds one of *P. lewisii* var. *intermedius*. It is planted at the lower end of the Weston Nursery of the Arboretum. It may be that the poorly drained soil in which it grows has altered its normal behavior. The plant was obtained in 1939 from F. L. Skinner, Dropmore, Manitoba, Canada. Nothing is known of its origin.

6. **Philadelphus** "Thelma" Hort.

A graceful little shrub, the bark castaneous, exfoliate; leaves ovate-lanceolate, 2–2.5 cm. long, 5–10 mm. wide, acute or rounded at the base, acute or shortly acuminate at the apex, sparsely strigose beneath, entire or faintly serrate, each side with 2 or 3 small sharp teeth; flowers ternate, rarely 5; corolla campanulate, 1.5 cm. across, the petals obovate, 9 mm. long.

CULTIVATED: Arnold Arboretum *606–39*, *E. J. Palmer*, June 24, 1943 (A).

This form was distributed by F. L. Skinner, Dropmore, Manitoba, Canada, in 1939. Nothing is known about its origin. It shows the influence of *P. purpurascens*.

7. **Philadelphus × pendulifolius** Carr. in Rev. Hort. **1875:** 360. 1875. — Koehne in Gartenfl. **45:** 542. 1896. — Schneider, Ill. Handb. Laubh. **1**: 369. 1905. — Rehder, Man. Cult. Trees Shrubs 273. 1927, ed. 2, 267. 1940.

Philadelphus verrucosus var. *pendulifolius* Moore in Bailey, Stand. Cycl. Hort. **5**: 2581. 1916.

Philadelphus latifolius pendulifolius Schnelle ex Beissner et al., Handb. Laubh. 127. 1903. — Starcs. in Darzkobibas Rokstu **1**: 122. 1925.

An upright shrub about 2 m. high, the branches erect, ramified and nodulous, the second year's growth castaneous, closed, the current year's growth glabrous or glabrescent. Leaves glossy, pendulous, ovate or broad-elliptic, 5–11 cm. long, 3–7 cm. wide, obtuse or rounded at the base, acuminate at the apex, subentire or faintly serrate, glabrous above, uniformly strigose-pilose beneath. Flowers 5 or 7, the lower pairs in the axils of

normal leaves; hypanthium and calyx densely strigose-villose, the hairs erect; sepals ovate, 5 mm. long; corolla cup-shaped, 2.5–2.8 cm. across, the petals obovate, 1.2 cm. long; stamens sterile, the disc glabrous, the style equal to or longer than the stamens, the apical end twisted in the bud. Capsules turbinate, the persistent sepals supermedian. Seeds long-caudate.

CULTIVATED: **Europe:** Hort. Plantière. *C. K. Schneider*, Sept. 1903 (A); Hort. Späth, *C. K. Schneider*, in 1902 (A). **United States:** Arnold Arboretum *5315*, without collector, Sept. 10, 1913 (A); *A. Rehder*, July 5, 1917 (A); *G. M. Merrill*, June 22, 1923 (BH); *S. Y. Hu*, June 12, 1951 (A); *5311*, *E. J. Palmer*, June 11, 1936 (A); Highland Park, *R. E. Horsey*, Oct. 2, 1917 (BH).

This noteworthy hybrid was raised from the seed collected by Billiard from a *Philadelphus* called "Fontenea-aux-roses." Koehne interpreted it as a hybrid of *P. pubescens* and *P. laxus*. Rehder doubtfully accepted this assumption. It is closely related to *P. pubescens*. As to the other parent, I think the influence of *P. inodorus* var. *carolinus* is very evident. The nodulous stems give one the impression of some insect or fungus infection. It is a very rare specimen. The Arnold Arboretum obtained this plant from the Späth Nursery in 1906.

8. **Philadelphus × polyanthus** Rehder in Jour. Arnold Arb. 1: 201. 1920; Man. Cult. Trees Shrubs 279. 1927, ed. 2, 274. 1940; et Bibl. Cult. Trees Shrubs 194. 1949.

An erect shrub, the bark castaneous, closed, tardily exfoliate, the current year's growth sparsely villose; leaves ovate, 3.5–5 cm. long, 1.5–2.5 cm. wide, rounded or obtuse at the base, acuminate at the apex, entire or with 1–3 sharp teeth on each side, glabrous above, sparsely strigose-pilose beneath; flowers 3 or 5, cymose or corymbose, the pedicels of the lower flowers elongated, sometimes branched; hypanthium and sepals uniformly pubescent, the sepals ovate, caudate at the apex, 5–8 mm. long; corolla cruciform, 3 cm. across, the petals oblong, 1.5 cm. long, 1 cm. wide.

CULTIVATED: **Europe:** Hort. Plantière, *C. K. Schneider*, June 26, 1906 (A). **United States:** Arnold Arboretum *4158*, without collector, June 22, 1903 (A); *S. Y. Hu*, June 1951 (A).

Rehder designated "Gerbe de neige" as the type form of this hybrid. The plant in the Arnold Arboretum was introduced from the Lemoine Nursery in 1900.

The following forms all have pubescent hypanthia. They should be placed here: "Atlas," "Boule d'argent," "Favorite," "Mont Blanc," "Norma," "Pavillon blanc," and "Van Houttei."

8a. **Philadelphus** "Atlas" Lemoine, Cat. 197: 17. 1923.

Bark castaneous, opaque, closed, with transverse cracks; the current year's growth glabrous; leaves ovate, (3–) 6–9 cm. long, 3–6 cm. wide,

obtuse at the base, shortly acuminate at the apex, glabrous above, uniformly strigose-pilose beneath; flowers 5 or 7, racemose, the hypanthium and sepals sparsely strigose-villose; sepals ovate, 5–6 mm. long; corolla cruciform, 3.5 cm. across, the petals oblong, 1.5 cm. long, 9–10 mm. wide; stamens fertile; disc and style glabrous.

CULTIVATED: Arnold Arboretum *21387*, *E. J. Palmer*, June 11, 1936 (A).

The Arnold Arboretum got this plant from the Morton Arboretum, Lisle, Ill. In the size of the flowers, the indumentum of the hypanthium, and the shape of the corolla, this form resembles *P.* "Gerbe de neige." It can be distinguished from the latter by its racemose inflorescence. The flowers of *P.* "Gerbe de neige" are three in a cyme or five in a corymb. Arnold Arboretum *19539* labeled *P.* "Atlas" is *P. floridus*. The flowers of that specimen are disciform.

8b. **Philadelphus** "Boule d'argent" Lemoine, Cat. 125: 11. 1893.—Rehder, Man. Cult. Trees Shrubs 279. 1927, ed. 2, 273. 1940.

Bark castaneous, tardily exfoliate, the current year's growth sparsely villose, glabrescent; leaves ovate, 3–4.5 cm. long, 1.5–2 cm. wide, rounded at the base, acute at the apex, glabrous above, very sparsely pilose on the primary nerves beneath; flowers double, 3 or 5, cymose, the pedicels of the lateral flowers 3–5 times longer than that of the center one, the hypanthium sparsely pilose; sepals glabrous, ovate, acuminate, 5–6 mm. long; corolla double, 3.5 mm. across.

CULTIVATED: **Europe:** Hort. Plantière, *C. K. Schneider*, June 26, 1906 (A). **United States:** Arnold Arboretum *4155*, without collector, June 21, 1916 (A).

The flower of this form reminds one of that of *P. coronarius* var. *dianthiflorus*, but it can be distinguished from the latter by its ternate or cymose flowers.

8c. **Philadelphus** "Favorite" Hort. ex Rehder, Man. Cult. Trees Shrubs 279. 1927, ed. 2, 274. 1940.

Bark gray or brown, closed or tardily exfoliate, the current year's growth sparsely villose; leaves ovate, 1.5–3 cm. long, 0.5–2 cm. wide, glabrous above, rounded or obtuse at the base, acute or shortly acuminate at the apex, uniformly strigose-pilose beneath; flowers 3 or 5, crowded, the hypanthium and sepals strigose-pilose; corolla cruciform, 3.5 cm. across, the petals obovate-oblong, 1.2 cm. long, 1 cm. wide; stamens all fertile; disc and style glabrous; capsules ellipsoid; seeds long-caudate.

CULTIVATED: Arnold Arboretum *8093*, *A. Rehder*, June 23, 1919 (A); *449–41*, *E. J. Palmer*, June 24, 1943 (A); Highland Park, *Mrs. R. E. Horsey*, June 16, 1918 (BH), Sept. 4, 1918 (BH).

The plants in the Arnold Arboretum are from two sources. Arnold Arboretum *8093* was from the Rochester Park Department, and no. *449–41* was from the H. Kohankie Nursery, Painesville, Ohio.

This form shows strongly the influence of *P. pubescens* Loisel. Its origin is not known.

8d. **Philadelphus** "Mont Blanc" Lemoine, Cat. **134**: 5. 1896, **188**: 12. 1915. — Rehder, Man. Cult. Trees Shrubs 279. 1927, ed. 2, 274. 1940.

Bark castaneous, closed, tardily exfoliate, the current year's growth strigose-pilose, the hairs with thickened bases; leaves ovate, 1.8–3 cm. long, 8–18 mm. wide, entire or with 1 or 3 teeth on the middle of each side, glabrous above, very sparsely and partially pilose beneath; flowers 3, 5, rarely 1, the hypanthium strigose-pilose; sepals glabrous; corolla cruciform, 2.5 cm. across, the petals obovate-oblong, 11 mm. long, 8 mm. wide; stamens fertile; disc and style glabrous.

CULTIVATED: Arnold Arboretum *4157*, *A. Rehder*, July 2, 1918 (A).

Rehder placed this form in *P.* × *lemoinei*. Its pubescent hypanthium suggests a closer relationship with *P.* × *polyanthus*.

8e. **Philadelphus** "Norma" Lemoine, Cat. **173**: 33. 1909, **188**: 12. 1915. — Rehder in Jour. Arnold Arb. **1**: 202. 1920; et Man. Cult. Trees Shrubs 280. 1927, ed. 2, 274. 1940.

Bark grayish brown, closed, tardily wearing off, the current year's growth strigose-pilose; leaves ovate, 3–5 cm. long, 1.2–3 cm. wide, rounded or obtuse at the base, acuminate at the apex, glabrous above, partially pilose beneath, serrate; flowers 5, rarely 3, the hypanthium and sepals sparsely villose; sepals ovate, caudate, 9 mm. long; corolla disciform, semidouble, 4–4.5 cm. across, the petals suborbicular, 14–18 mm. in diameter; stamens fertile; disc and style glabrous.

CULTIVATED: Arnold Arboretum *7595*, without collector, July 2, 1917 (A); *G. M. Merrill*, June 22, 1923 (BH); *930–29*, *E. J. Palmer*, June 11, 1936 (A); *19265*, *E. J. Palmer*, June 11, 1936 (A), *E. R. Sears*, June 21, 1935 (BH), Sept. 13, 1935 (BH); Highland Park, *R. E. Horsey*, June 16, 1918 (BH), Sept. 4, 1918 (BH).

Rehder placed this form under *P.* × *cymosus* in his manual. The type form of that hybrid has a glabrous hypanthium. As *P.* "Norma" has a pubescent hypanthium, it is better to place it under *P.* × *polyanthus*, which is characterized by a pubescent hypanthium.

This form was introduced on two occasions from the Lemoine Nursery, once in 1913 and the second time in 1925. The first introduction carries the field number *7595* and the second *19265*. Arnold Arboretum *930–29* was made from a cutting of *7595*. The disciform flower and the indumentum on the hypanthium of these plants remind one of *P. floridus* Beadle.

8f. **Philadelphus** "Pavillon blanc" Lemoine, Cat. **134**: 5. 1896, **148**: 33. 1901. — Rehder in Jour. Arnold Arb. **1**: 201. 1920; et Man. Cult. Trees Shrubs 279. 1927, ed. 2, 274. 1940.

Bark castaneous, closed, tardily wearing off, the current year's growth strigose-pilose; leaves ovate, 1.7–3.5 cm. long, 1–1.8 cm. wide, entire, obtuse at the base, acute at the apex, glabrous above, uniformly strigose-pilose beneath; flowers 5, 7, or 3, the hypanthium and sepals uniformly strigose-villose; corolla cruciform, 3.5–4 cm. across, the petals oblong, 17 mm. long, 11 mm. wide, erose at the apex; stamens largely sterile, the anthers mucronate at the apex; disc and style glabrous.

CULTIVATED: Arnold Arboretum *4153*, without collector, June 27, 1904 (A), June 29, 1906 (A); *S. Y. Hu*, June 22, 1951 (A).

This form was introduced to the Arnold Arboretum in 1900. The plant, numbered 4153, flowered in 1904. It is a low mound-shaped shrub. The flowers are fragrant.

8g. **Philadelphus** "Van Houttei" Hort. ex Bean in Kew. Hand-list ed. 4, 199. 1934, *nom. nud.*

Bark nigrescent, closed; the current year's growth sparsely scabrous-villose, glabrescent; leaves oblong-ovate, 5–7 cm. long, 2.5–3 cm. wide, obtuse at the base, acuminate at the apex, partially hirsute and becoming glabrescent above, rather densely and uniformly scabrous-villose beneath; flowers 3 or 9, the lower pair in the axils of normal leaves, cymose, the peduncles 11–22 mm. long; hypanthium and sepals incanously strigose-pilose, the hairs appressed; sepals foliaceous, ovate, caudate, 8–16 mm. long; corolla disciform, 3.5 cm. across, the petals ovate-orbicular, 1.5 cm. long, 1.4 cm. wide; stamens fertile; disc and style glabrous.

CULTIVATED: Arnold Arboretum *19572*, *E. J. Palmer*, June 11, 1939 (A).

The Arnold Arboretum obtained this plant from Kew in 1925. Nothing is known about its parentage. It shows strongly the influence of *P. pubescens* Loisel. and *P. floridus* Beadle.

9. **Philadelphus × burkwoodii** Hort. ex Gard. Chron. III. 89: 438. 1931.

Bark nigrescent, closed, slowly exfoliate, the current year's growth strigose-pilose, the hairs with thickened bases, the axillary buds exposed. Leaves ovate or ovate-elliptic, those on the vegetative branches 3.5–6.5 cm. long, 1.5–3 cm. wide, those on the flowering branches 1.5–3.5 cm. long, 0.6–1.5 cm. wide, obtuse at the base, acute or shortly acuminate at the apex, glabrous above, sparsely strigose-pilose beneath. Flowers 1, 3, or rarely 5, the sepals and hypanthium sparsely, sometimes partially pilose, the hairs appressed; sepals ovate, caudate, 8–15 mm. long; corolla cruciform, 4.5 cm. across, the petals obovate-oblong, 2.1 cm. long, 1.2 cm. wide, sparsely pilose on the inside; stamens fertile; disc and style glabrous, divided almost to the base, the stigmata clavate. Capsule ellipsoid, pointed at both ends, the persistent sepals circumferential.

CULTIVATED: **Europe:** Kew *109.30* (Burkwood), *R. Melville*, June 22, 1937 (A), Sept. 10, 1937 (A). **United States:** Arnold Arboretum *864–34*, *E. J. Palmer*, Sept. 1, 1939 (A), July 9, 1940 (A).

As recorded in Gardener's Chronicle, this cultivar was a product of a cross between *P.* "Étoile rose" and *P.* "Virginal." Its exposed axillary buds and its pubescent petals suggest a relationship with *P. mexicanus*. The plant in the Arnold Arboretum was raised from a cutting obtained from Mrs. J. Norman Henry, Gladwyne, Penn. The inside of the petals of that plant is not hirtellous.

10. **Philadelphus** × **virginalis** Rehder in Jour. Arnold Arb. 1: 202. 1920; et Man. Cult. Trees Shrubs 280. 1927, ed. 2, 274. 1940.

Erect shrubs of medium height, 1–2.5 m. high, the branches stiff, upright, the bark of the second year's growth gray, closed, tardily wearing off, the current year's growth sparsely villose, glabrescent. Leaves ovate, 4–7 cm. long, 2.5–4.5 cm. wide, rounded at the base, shortly acuminate at the apex, glabrous or glabrescent above, uniformly strigose-villose beneath. Inflorescence racemose, the lower pairs in the axils of normal leaves, rarely ternate; hypanthium and sepals uniformly strigose-villose or incanous, the flowers double. Capsules subglobose or ellipsoid. Seed when present medium caudate, the testa brown.

This hybrid was typified by the cultivar *P.* "Virginal." It is characterized by the rather large ovate villose leaves, the double racemose flowers, and the pubescent hypanthium and calyx. It should also include the following forms: "Argentine," "Boule d'argent," "Enchantment," "Fleur de neige," "Glacier," "Le Roi," and "Pyramidal." They show the influence of *P. pubescens* Loisel. so much that they may be regarded as the double-flowered garden forms of that species.

10a. **Philadelphus** "Argentine" Lemoine, Cat. **185**: 5. 1913, **188**: 12. 1915. — Rehder, Man. Cult. Trees Shrubs 280. 1927, ed. 2, 274. 1940.

Bark gray, closed, the current year's growth glabrous; leaves broad-ovate, 3–4.5 cm. long, 1.5–3 cm. wide, subentire or with 2, 3, or 4 teeth on each side, rounded at the base; flowers ternate, rarely 5 or 1; corolla 4–4.5 cm. across, the petals numerous, about 30, rounded or obtuse at the apex.

CULTIVATED: Arnold Arboretum *7074*, without collector, June 26, 1916 (A); *7074–1*, *E. J. Palmer*, June 18, 1936 (A); *203–38*, *E. J. Palmer*, Sept. 19, 1940 (A); *S. Y. Hu*, June 15, 1951 (A).

Arnold Arboretum *7074* was introduced directly from the Lemoine Nursery. It is a genuine form. Arnold Arboretum *203–38* was from Wilhelm Pfitzer, Stuttgart, Germany.

10b. **Philadelphus** "Enchantment" Lemoine, Cat. **197**: 18. 1923.

Bark nigrescent, closed, the current year's growth villose; leaves ovate, 3–5 cm. long, 1.2–3 cm. wide, obtuse or rounded at the base, acute or shortly acuminate at the apex, serrate; flowers 7 or 9, the corolla 2.5 cm. across, the outer petals rounded and the inner ones acute.

CULTIVATED: Arnold Arboretum *19534*, *E. J. Palmer*, June 11, 1936 (A); *21996*, *E. J. Palmer*, June 11, 1936 (A); *21881*, *E. J. Palmer*, June 23, 1938 (A).

The first cited specimen was introduced in 1925 from the Chenault Nursery, Orléans, France. The last was obtained from the Lemoine Nursery in 1932.

10c. **Philadelphus** "Fleur de neige" Lemoine, Cat. **189**: 20, *t.* [*2*]. 1915.

Lemoine described this form as having "the appearance of *P. inodorus* var. *grandiflorus* with large semidouble flowers covering the whole shrub with a mantle of snow." The plant in the Arnold Arboretum bearing this name was obtained as cuttings from the Park Department, Rochester, N. Y. It has simple flowers and does not match Lemoine's illustration. It does not represent the genuine "Fleur de neige."

10d. **Philadelphus** "Glacier" Lemoine, Cat. **185**: 5. 1913, **188**: 12. 1915.

Bark gray, closed; the current year's growth glabrous; leaves generally small, 2.5–3.5 cm. long, 1.2–2.5 cm. wide, rounded or subcordate at the base, obtuse or acute at the apex, serrate; flowers fragrant, 7, 9, or 5, the corolla 2.5 cm. across, the petals obtuse or acute at the apex.

CULTIVATED: Arnold Arboretum *7075*, without collector, July 2, 1917 (A); *7075–2*, *E. J. Palmer*, June 11, 1938 (A); *19263*, *E. J. Palmer*, June 11, 1936 (A).

This entity flowers late. Its fragrant flowers last for a long time on the plant. It is a very desirable form for small gardens. All the Arnold Arboretum plants were introduced from the Lemoine Nursery. They are true to the type.

10e. **Philadelphus** "Girandole" Lemoine, Cat. **189**: 20, *t.* [*3*]. 1915. — Silva Tarouca, Freil.-Laubgeh. 257, *fig. 307*. 1930.

Bark castaneous, exfoliate, the current year's growth pilose; leaves ovate, 2.5–4.5 cm. long, 1.3–2.3 cm. wide, subentire or with 1–6 teeth on each side, rounded at the base, acute or shortly acuminate at the apex, uniformly pilose on both surfaces; flowers 5 or 7, racemose, the hypanthium and sepals sparsely pilose; sepals long-caudate, 7–10 mm. long; corolla double, 3.5 cm. across; petals rounded at the apex; stamens all sterile.

CULTIVATED: Arnold Arboretum *19262*, *E. J. Palmer*, June 11, 1936 (A), *S. Y. Hu*, June 8, 1951 (A).

This plant was introduced into the Arnold Arboretum in 1925. It came from the Lemoine Nursery, Nancy, France.

10f. **Philadelphus** "Le Roi" Hort.

A very low shrub up to 1 m. high, the bark nigrescent, closed, tardily wearing off, the current year's growth glabrous; leaves ovate or ovate-elliptic, 2–5 cm. long, sparsely strigose-pilose on both surfaces; flowers double, 5 or 7, racemose.

CULTIVATED: Arnold Arboretum *516–51, S. Y. Hu*, June 1954 (A), Nov. 1, 1954 (A).

This form was distributed by the Cole Nursery of Ohio. Nothing is known of its origin. It resembles *P.* "Virginal" but had more uniform flowers and a lower habit.

10g. **Philadelphus** "Pyramidal" Lemoine, Cat. **192**: 21. 1919.

Bark grayish brown, closed, the current year's growth glabrescent; leaves broad-ovate 3–6 cm. long, 2–4 cm. wide, denticulate, rounded or subcordate at the base, shortly acuminate at the apex; flowers 7 or 5, the corolla 3 cm. across, the outer petals suborbicular, 1.2 cm. diameter.

CULTIVATED: Arnold Arboretum *19266, E. J. Palmer*, June 22, 1938 (A), *S. Y. Hu*, June 14, 1951 (A); *1099–28, Kobuski & Roush*, Sept. 10, 1931 (A); *22025, E. J. Palmer*, June 11, 1936 (A).

This form was introduced into the Arnold Arboretum in 1925 from the Lemoine Nursery. That specimen bears the field number *19266*.

10h. **Philadelphus** "Virginal" Lemoine, Cat. **173**: VI, *t.* [*6*]. 1909, **188**: 13. 1915. — Bean, Trees Shrubs ed. 7, **2**: 415. 1950.

Bark gray, tardily wearing off, the current year's growth glabrous; leaves ovate, rather large, 4–8 cm. long, 3–4.8 cm. wide, obtuse at the base, serrate, with 1–4 teeth on each side; flowers 7, 9, rarely 5 or 3, the corolla various, semi-double, double, or on some branches simple, 3–4 cm. across, the outer petals obovate, 1.2–2 cm. long, rounded at the apex.

CULTIVATED: Arnold Arboretum *7596, A. Rehder*, July 2, 1918 (A); *E. J. Palmer*, June 11, 1936 (A); *15424, C. K. Allen*, June 21, 1927 (A).

Lemoine announced this form as a variety of the first class. Bean also considered it as the finest form in the genus and mentioned the award of the first class certificate in 1911 by the Royal Horticultural Society, London. But the plant in the Arnold Arboretum has a very irregular growth. Many branches are over-vigorous in vegetative growth and bear no flowers. Various parts of the same plant bear different flowers, some being simple while others are double. It is interesting but not very desirable for small gardens.

11. **Philadelphus × maximus** Rehder in Mitt. Deutsch. Dendr. Ges. **1913** (*22*): *255*. [1914]; et Man. Cult. Trees Shrubs *276*. 1927, ed. *2*, *270*. 1940. — Moore in Bailey, Stand. Cycl. Hort. **5**: *2582*. 1916.

A tall shrub up to 5 m. high, the principal branches 5 cm. in diameter, bark of the second year's growth light gray, closed, the current year's growth glabrescent. Leaves ovate or ovate-elliptic, on the vegetative shoot 8–12 cm. long, 4–6.5 cm. wide, on the flowering shoot 6–8 cm. long, 3–4 cm. wide, rounded, obtuse or rarely cordate at the base, acuminate at the apex, subentire or faintly denticulate, sparsely hirsute above, tomentose beneath. Flowers 7 or 9, the lower pairs in the axils of normal leaves; hypanthium and sepals sparsely scabrous-pilose, the hairs partly erect; sepals ovate, 5 mm. long, acute or shortly acuminate; corolla cruciform, 3–3.5 cm. across, the petals obovate, 13 mm. long; stamens 26, the anthers sterile; disc and style glabrous, the stigmata clavate.

CULTIVATED: Arnold Arboretum *6606*, *A. Rehder*, June 24, 1913 (A, TYPE); *6606–1* = *15373*, without collector, June 21, 1916 (A).

This plant was received from Kew in 1885 as *P. tomentosus*. It was probably a hybrid produced accidentally in that garden. Its robust stems and great height show hybrid vigor. Its completely sterile stamens indicate the disturbed chromosomes. Rehder was probably right in assuming it to be a hybrid between *P. pubescens* and *P. tomentosus*. It is a very rare specimen.

12. **Philadelphus × nivalis** Jacques in Hort. Univ. **2**: 19. 1841. — Rehder, Man. Cult. Trees Shrubs *273*. 1927, ed. *2*, *267*. 1940.

Philadelphus verrucosus var. *nivalis* (Jacques) Rehder in Jour. Arnold Arb. **1**: 199. 1920.

An arching shrub up to 2.5 m. high, the bark castaneous, exfoliate, the current year's growth glabrous. Leaves ovate or ovate-elliptic, 5–10 cm. long, 2.5–6 cm. wide, rounded or obtuse at the base, acuminate at the apex, subentire or faintly denticulate, glabrescent above, uniformly strigose-villose beneath. Flowers 5 up to 11, in interrupted racemes, the lower pairs in the axils of normal leaves; hypanthium and sepals scabrous-villose, the hairs dense, long, and partly erect; sepals ovate, acuminate, 7 mm. long; corolla disciform, 2.5–3.5 cm. across, the petals suborbicular, 1.3–1.5 cm. in diameter; stamens all fertile; disc and style glabrous.

CULTIVATED: **Europe:** Kew, *G. Nicholson 2596* (A). **United States:** Arnold Arboretum, *C. E. Faxon*, June 16, 1911 (A); *15356–1–A*, *E. J. Palmer*, June 11, 1936 (A); *22026*, *E. J. Palmer*, June 11, 1936 (A), *S. Y. Hu*, June 14, 1951 (A); vicinity of the Arnold Arboretum, Orchard St., *A. Rehder*, June 21, 1910 (A); Eliot St., *C. E. Faxon*, June 20, 1911 (A); Hort. C. S. Sargent, *A. Rehder*, June 22, 1910 (A).

This cultivar is assumed to be a hybrid of *P. coronarius* Linn. and *P. pubescens* Loisel. It is one of the most commonly cultivated *Philadel-*

phus in the gardens of Boston. Rehder in his Manual mentioned a double-flowered form, *P.* × *nivalis* f. *plenus* (Späth) Rehder. I have not seen any specimen of this form.

13. **Philadelphus × congestus** Rehder in Jour. Arnold Arb. 1: 200. 1920; Man. Cult. Trees Shrubs 280. 1927, ed. 2, 268. 1940; et Bibl. Cult. Trees Shrubs 192. 1949.

An arching shrub, the bark castaneous, exfoliating, the current year's growth pubescent; leaves elliptic, 3–3.5 cm. long, 1–2.5 cm. wide, acute at both ends or shortly acuminate at the apex, uniformly strigose-pilose beneath, the hairs appressed; flowers 5 in short racemes, rarely 3 or solitary, the hypanthium sparsely pilose, the corolla subdisciform, 3 cm. across, the petals obovate.

CULTIVATED: Arnold Arboretum *5854*, *A. Rehder*, June 24, 1912 (A, TYPE); *349–29*, *E. J. Palmer*, Aug. 18, 1936 (A), June 22, 1938 (A).

This species originated in the Späth Nursery near Berlin and was distributed as *P. inodorus speciosus grandiflorus*. The parents are probably *P. inodorus* var. *laxus* and *P. pubescens* var. *verrucosus*. Arnold Arboretum *349–29* was distributed by the Vilmorin Nursery as "*P. Yokohamae*."

14. **Philadelphus × monstrosus** (Späth) Schelle in Beissner et al., Handb. Laubh.-Ben. 129. 1903, *nom. subnud.* — Rehder in Jour. Arnold Arb. 1: 199. 1920; et Man. Cult. Trees Shrubs 273. 1927, ed. 2, 268. 1940.

Philadelphus gordonianus monstrosus Hort. ex. Späth. Kat. **100:** 95. 1897, *nom. nud.*

A moderately tall shrub about 2 m. high; bark of the second year's growth gray, closed, the current year's growth glabrous or glabrescent. Leaves ovate, rarely ovate-elliptic, 3.5–9 cm. long, 2.5–5.5 cm. wide, partially sparsely strigose-pilose above, uniformly strigose-villose beneath. Flowers 7 or 9, racemose, the lower pairs in the axils of normal leaves; hypanthium sparsely weak-villose, the hair almost erect; corolla cruciform, 3.5–4 cm. across, the petals oblong; stamens all fertile, the disc glabrous, the style glabrous or with a few hairs at the base, the style half divided, the stigma spatulate. Capsule turbinate, the persistent calyx supermedian. Seeds long-caudate.

CULTIVATED: Arnold Arboretum *6965*, *A. Rehder*, July 3, 1917 (A, TYPE); *6965–2 = 5881*, *A. Rehder*, June 18, 1918 (A); *6965–3 = 15373*, *A. Rehder*, July 18, 1918 (A); *6965–4 = 15374*, *E. J. Palmer*, June 14, 1921 (A).

This taxon was distributed by the Späth Nursery as *P. gordonianus monstrosus*. Rehder assumed it to be a hybrid between *P. lewisii* var. *gordonianus* and *P. pubescens*. It differs from *P. pubescens* only in having a less densely pubescent hypanthium.

15. **Philadelphus** "Slavinii" Hort. ex Wyman, Shrubs Vines Am. Gard. 422. 1949. *nom. nud.*

A tall mound-shaped shrub 3 m. high with arching and drooping branches, the bark castaneous, exfoliate, the current year's growth glabrous. Leaves elliptic or ovate-elliptic, 6.5–9.5 cm. long, 2–3.5 cm. wide, acute at the base, acuminate at the apex, glabrous above, uniformly strigose-pilose beneath, subentire or with 2–5 teeth on each side. Flowers 5, crowded, rarely 3 or 1; hypanthium and sepals uniformly strigose-villose; sepals ovate, acuminate, 7 mm. long; corolla cruciform, 4–6 cm. across, the petals oblong, rounded at the apex; disc and style glabrous. Capsules ellipsoid. Seeds long-caudate.

CULTIVATED: Arnold Arboretum *1067–36, E. J. Palmer*, June 24, 1936 (A), Oct. 18, 1938 (A), Sept. 29, 1940 (A); *S. Y. Hu*, Nov. 1, 1954 (A).

This plant resembles *P. inodorus* var. *grandiflorus* in the tall, mound-shaped habit, serrate, ovate-elliptic leaves, and large flowers. But it can be readily distinguished by its pubescent hypanthium. In the Arnold Arboretum, also, it flowers two or three weeks later than *P. inodorus* and its varieties. When in full bloom the entire plant is covered with white balls of flowers. In my opinion it is a very superior specimen. The Arnold Arboretum obtained the specimen from Mrs. W. W. Gibbs, Staunton, Virginia, in the form of cuttings in 1936. Nothing is known about its origin.

16. **Philadelphus** "Stenopetala" Carr. in Rev. Hort. **1870**: 340. 1870. — Moore in Bailey, Stand. Cycl. Hort. **5**: 2582. 1916.

Bark castaneous or nigrescent, closed; leaves ovate, 4–7.5 cm. long, 1.8–3 cm. wide, obtuse at the base, acuminate at the apex, faintly serrate, uniformly strigose-pilose beneath; flowers 5 or 7, racemose, the hypanthium and sepals sparsely pilose; corolla subcampanulate, 1.5 cm. across, the petals oblanceolate, 8 mm. long, 3 mm. wide, obtuse or rounded at the apex, glabrous inside.

CULTIVATED: Hort. Miss L. C. Crehore, Moss Hill, Jamaica Plain, Mass., *J. G. Jack*, June 22, 1926 (A).

The narrow petals and stellate corolla of this form suggest some relationship with *P. falconeri*. But the glabrous petals, pubescent hypanthium, and racemose inflorescence are very distinctive. In *P. falconeri* the corolla is hirtellous on the inside, the hypanthium glabrous, and the pedicels of the lower pairs of flowers are elongated and sometimes divided, giving the inflorescence the appearance of a corymb. It may be a mutant of *P. pubescens*.

17. **Philadelphus** "Maculiflorus" Koehne ex Schneider, Ill. Handb. Laubh. **1**: 363. 1905, **2**: 929. 1912. — Rehder, Man. Cult. Trees Shrubs 280. 1927, ed. 2, 274. 1940.

Bark castaneous, exfoliate, current year's growth glabrous. Leaves ovate or ovate-elliptic, 5–8 cm. long, 2–5 cm. wide, rounded or obtuse at the base, barbate, and on the primary nerves pubescent, denticulate, with 5–9 teeth on each side. Flowers 7 in loose racemes, the lower pairs in the axils of normal leaves; pedicels 7–12 mm. long; hypanthium and sepals glabrous; corolla subdisciform, 3 cm. across, the petals obovate, 1.3 cm. long, reddish at the base; stamens ca. 35; all fertile; style and disc glabrous. Capsules turbinate, 7 mm. long, 6 mm. in diameter.

CULTIVATED: **Europe:** Bot. Gart. Leipzig, *A. Rehder 3121* (A); Hort. Bot. Dresden, *C. K. Schneider*, June 25, 1904 (A, type material).

This form is apparently a bud mutant of *P. coronarius*. It is not known in American gardens and may now be non-existent in European gardens as well.

18. **Philadelphus × purpureo-maculatus** Lemoine, Cat. **152**: VIII. 1902. — Hemsl., Bot. Mag. **134**: *t. 8193*. 1908. — Wayland in Gard. **82**: 267, *fig.* 1918, **84**: 336, *fig.* 1920. — Rehder in Jour. Arnold Arb. 1: 203. 1920; et Man. Cult. Trees Shrubs 280. 1927, ed. 2, 274. 1940. — A. O[sborn] in Gard. **87**: 396, *fig.* 1923, **89**: 652, fig. 1925. — Jeffery in Gard. Chron. **113**: 104, *fig. 55*. 1943.

Philadelphus × *phantasia* Moore in Bailey, Stand. Cycl. Hort. **5**: 2582. 1916. *Philadelphus lemoinei* var. *maculatus* Gard. Chron. III. **36**: 140. 1904.

Bark nigrescent, closed, slowly wearing off; current year's growth pubescent. Leaves broad-ovate, 1–3.5 cm. long, 0.6–2.5 cm. wide, rounded at the base, acute at the apex, entire or with 1 or 2 teeth on each side, very sparsely pilose beneath. Flowers solitary, the hypanthium and base of the sepals partially strigose-pilose; sepals leafy, ovate, 7 mm. long; corolla disciform, 2.5–3 cm. across, the petals ovate, 11 mm. long, 10 mm. wide, purplish red at the base. Capsules ellipsoid, 6 mm. long, 5 mm. in diameter, the persistent sepals circumferential.

CULTIVATED: **Europe:** Bot. Gart. Forstakadamie *57*, *H. Zabel*, June 29, 1905 (A). **United States:** Arnold Arboretum *1102–28*, *Kobuski & Roush*, Sept. 30, 1931 (A); Highland Park, New York, *R. E. Horsey*, Sept. 4, 1918 (BH); Garden of A. & A. Blake, Berkeley, California, *N. F. Bracelin 2522* (BH).

Lemoine in 1900 made a cross between *P. microphyllus* and a purple-centered *Philadelphus* which was horticulturally known as *P. coulteri*, not Watson, and produced *P.* "Fantaisie" (Lemoine Cat. **146**: X. 1900). From the seed of this horticultural form he raised *P.* × *purpureo-maculatus*. I have not seen any specimen of *P.* "Fantaisie" and I doubt if it can be found in any American gardens. *Philadelphus* × *purpureo-maculatus* is also rare in America.

The flowers of the following forms have been reported to have purplish rose or pink centers: "Étoile rose," "Fantaisie," "Galathée," "Nuage rose," "Oeile de pourpre," "Roméo," "Sirène," "Surprise," and "Sylviane." These

forms are rare in American gardens. The information here presented is largely abstracted from the original descriptions, which were published in French and are not available in most botanical institutions in America.

Philadelphus "Belle étoile," *P.* "Bicolore" and *P.* "Sybille" were announced as offspring raised from seeds of *P.* × *purpureo-maculatis*. It has been discovered that they are forms with triploid chromosomes. They are not included here among the following diploid purple-eyed forms. At present these triploid forms are also rare in American gardens. They have large flowers and a late and long blooming season. Their purple-centered flowers are very attractive. Very likely they will soon gain popularity among growers.

18a. **Philadelphus** "Etoile rose" Lemoine, Cat. **173**: 24. 1909, **176**: 26. 1910, **188**: 12. 1915.

It was stated that this form came from a cross between *P.* "Fantaisie" and *P.* × *purpureo-maculatus*. It has large flowers and elongated petals which are white blotched with pink.

18b. **Philadelphus** "Fantaisie" Lemoine, Cat. **176**: X. 1900.

It was reported that this form was obtained through a cross between *P. coulteri* and a variety of *P. lemoinei*. It has large disciform flowers fringed at the margin, pure white, pale rose at the center.

18c. **Philadelphus** "Galathée" Lemoine, Cat. **188**: 12. 1915.

A shrub with long arching branches, medium-sized leaves, single cup-shaped flowers, white, slightly tinged in the center.

18d. **Philadelphus** "Nuage rose" Lemoine, Cat. **190**: 22. 1916.

A very free flowering shrub with small leaves, large fragrant flowers with slightly fringed petals, white with a broad center of soft flax-rose.

18e. **Philadelphus** "Oeile de pourpre" Lemoine, Cat. **177**: 7. 1911, **188**: 12. 1915.

A low shrub with small leaves, large, simple, cup-shaped flowers, the petals cream-white blotched with dark purple at the center.

18f. **Philadelphus** "Roméo" Lemoine, Cat. **185**: 37. 1913, **188**: 12. 1915.

A vigorously growing shrub, tufted and floriferous, with rather small scabrous leaves, medium-sized flowers with the petals cream-white, blotched wine-purple at the base.

18g. **Philadelphus** "Sirène" Lemoine, Cat. **176**: 26. 1910, **188**: 13. 1915.

Bark nigrescent, tardily wearing off, the current year's growth glabrous, axillary buds enclosed; leaves ovate-elliptic, 5–9.5 cm. long, 2.5–4 cm. wide, obtuse at the base, acuminate at the apex, glabrous above, sparsely

villose on the nerves beneath, remotely denticulate; flowers 3 or 5; capsules obovoid, slightly strigose-pilose.

CULTIVATED: Arnold Arboretum *1063–36, E. J. Palmer*, Sept. 25, 1940 (A).

This form is distinguished from the other purple-centered forms by its large leaves. The Arnold Arboretum obtained its plant from W. W. Gibbs, Staunton, Va., in 1936.

18h. **Philadelphus** "Surprise" Lemoine, Cat. **182**: 35. 1912, **188**: 13. 1915.

A shrub with rather large and well-presented flowers, the petals white blotched with carmine-purple at the base.

18i. **Philadelphus** "Sylviane" Lemoine, Cat. **191**: 21. 1917.

This form was announced as a superb cultivar with large, well-expanded flowers, the broad petals pure white suffused with pale pink at the base.

19. **Philadelphus** "Bicolore" Lemoine, Cat. **192**: 21. 1919. — Janaki Ammal in Jour. Hort. Soc. London **76**: 273. 1951.

A low shrub 1 m. high; bark castaneous, tardily exfoliate, the current year's growth sparsely villose, the axillary buds slightly exposed. Leaves ovate or oblong-ovate, 2.5–4 cm. long, 1–2 cm. wide, obtuse at the base, acuminate at the apex, with 1, 2, or 3 teeth at the middle of each side, slightly hirsute above, uniformly strigose-pilose beneath. Flowers solitary, rarely ternate, the hypanthium and sepals uniformly sparsely strigose-villose; sepals foliaceous, ovate-lanceolate, 11 mm. long, 4 mm. wide at the base; corolla subcampanulate, 4.5–5 cm. across, the petals ovate or suborbicular, 2.2 cm. long, 1.8 cm. wide; hirtellous on the inside; stamens ca. 29; disc and style glabrous. Capsules subglobose, 6 mm. in diameter. Seed long-caudate.

CULTIVATED: Arnold Arboretum *604–36, E. J. Palmer*, Oct. 13, 1938 (A); June 24, 1943 (A); *S. Y. Hu*, June 22, 1951 (A); *16222, E. J. Palmer*, June 22, 1938 (A).

The Arnold Arboretum obtained its plants from two sources, *604–36* from Kew in 1936, and *16222* from T. A. Havemeyer, Long Island, N. Y. The latter specimen was received as *P.* "Belle étoile." So far as I can detect, *P.* "Bicolore" is distinguished from *P.* "Belle étoile" by its fertile stamens and its petals being sparsely hirtellous on the inside. Arnold Arboretum *16222* is a typical *P.* "Bicolore."

This form is the most strikingly beautiful, and interesting *Philadelphus* in the Arnold Arboretum collection. From a distance the cup-shaped flowers appear white. A closer view shows that the petals are purple at the base, yellowish at the middle and white at the apical half. Exposed to open

pollination, from three to twenty percent of its seeds are fertile. Mr. Lewis Lipp, former Propagator at the Arnold Arboretum, collected the seeds in 1950. He raised ninety individuals, all from one mother plant. Being a triploid, in the formation of the gametes, the chromosomes are not evenly distributed. Thus the seeds of that plant carry different genomes, and the offspring show an enormous degree of variation in vitality, vigor, height, color, indumentum, shape, size, and dentation of the leaves, and in the size, type, and color of the flowers. Mr. Dexter R. Sampson, a graduate student of Dr. Karl Sax, has made a cytological survey of all the surviving individuals. He concluded that it is evident there is no correlation between the shape and dentation of the leaves and the chromosome number.[1]

When Lemoine announced this garden form, he did not give its origin. Janaki Ammal accredited it to the selfing of the diploid hybrid *P. purpureo-maculatus*. The shape of the petals and the indumentum on the leaves and hypanthium remind one of *P. floridus*, and the soft yellow hairs on the inside of the petals suggest a relationship with *P. mexicanus*.

20. **Philadelphus** "Belle étoile" Lemoine, Cat. 197: 18. 1923. — Janaki Ammal in Jour. Hort. Soc. London **76**: 273, *fig. 144*. 1951.

Bark castaneous, tardily exfoliate, the current year's growth sparsely villose, the axillary buds exposed. Leaves ovate, 1.5–4 cm. long, 1–2 cm. wide, rounded or obtuse at the base, shortly acuminate at the apex, sparsely hirsute above, uniformly strigose-pilose beneath. Flowers ternate or solitary, the hypanthium and sepals uniformly and sparsely villose; sepals ovate-lanceolate, 10–11 mm. long; corolla subcampanulate, 4.5–5 cm. across, the petals ovate, 2.2 cm. long, 1.8 cm. wide, glabrous on both surfaces; stamens ca. 27, the anthers sterile; the disc and style glabrous.

CULTIVATED: Arnold Arboretum *18535*, *E. J. Palmer*, June 22, 1938 (A); *21880*, *E. J. Palmer*, June 10, 1936 (A).

This is a comparatively more recent production. The Arnold Arboretum obtained its plants in 1925 and 1932 respectively; number *18535* was from the Chenault Nursery, Orleans, France, and no. *21880* came from the Lemoine Nursery. These specimens resemble *P.* "Bicolore" in the size of their leaves, in the indumentum, and the size and color of their flowers. Nevertheless this form can be distinguished from *P.* "Bicolore" by its sterile anthers and glabrous petals.

DOUBTFUL AND EXCLUDED SPECIES

Pochlaks and Zamelis in 1939 reported the creation of ten hybrids, giving botanical recognition to all of them. Some of the named parents, such as *P. falconeri*, are sterile hybrids, and others are invalid species. I am

[1] Dexter R. Sampson, Studies on the Progeny of the Triploid Philadelphus and Forsythia, in *Jour. Arnold Arb.* **36**: 369–384. 1955.

very doubtful about the identity of those parent plants. All the ten *nomina nuda* are listed here.

1. PHILADELPHUS ABELEI (*P. lewisii* × *P. verrucosus*) Pochlaks & Zamelis in Acta Horti Bot. Univ. Latv. **11–12:** 230. 1939, *nom. nud.*
2. PHILADELPHUS ARACHNOIDEUS Soland. ex Gaertn., Frut. Sem. Pl. **1:** 174. 1788, *nom. nud.* = *Leptospermum arachnoides* Gaertn. l.c. *t. 35, fig. 3.* 1788 = **L. arachnoideum** Seem. in Trans. Linn. Soc. **3:** 263. 1797. Native of Australia.
3. PHILADELPHUS ARBORESCENS Browne, Hist. Jam. 240. 1789. = **Eugenia uniflora** Linn., Sp. Pl. 470. 1753. Native of Jamaica.
4. PHILADELPHUS AROMATICUS Ait., Hort. Kew. ed. 1, **2:** 156. 1789 = **Leptospermum ericoides** A. Rich., Bot. Voy. Astrol. **1:** 338. 1832. Native of New Zealand.
5. PHILADELPHUS CORYMBOSUS Wall., Num. List 3652. 1829 **Deutzia staminea** R. Br. ex Wall., Num. List 3651. 1829; et Pl. As. Rar. **2:** 82, *t. 191.* 1831.
6. PHILADELPHUS FLORIBUNDUS Usteri in Roemer & Usteri, Mag. Bot. 3 (7): 177, *t. 2.* 1790 = **Leptospermum scoparium** Forster, Char. Gen. Pl. 72, *t. 36.* 1776. Native of New Zealand.
7. PHILADELPHUS GALENICKII (*P. acuminatus* × *P. magdalenae*) Pochlaks & Zamelis in Acta Horti Bot. Univ. Latv. **11–12:** 230. 1939, *nom. nud.*
8. PHILADELPHUS IMBRICATUS Soland. ex Gaertn., Fruct. Sem. Pl. **1:** 175. 1788 = **Baeckea crenulata** D.C., Prodr. **3:** 230. 1828. Native of Australia.
9. PHILADELPHUS JANSONII (*P. latifolius* × *P. verrucosus*) Pochlaks & Zamelis in Acta Horti Bot. Univ. Latv. **11–12:** 231. 1939.
10. PHILADELPHUS KETELÊERII Carr. in Rev. Hort. **1866:** 44. 1866. Carrière recorded that the plant which this name represented was raised from seed of *P. coronarius* cultivated in the grounds of the Museum of Natural History in Paris. It has double or semidouble flowers with pointed petals fringed or dentate at the apex. It is very doubtful whether this form is still in existence.
11. PHILADELPHUS LAEVIGATUS Soland. ex Gaertn. Fruct. Sem. Pl. **1:** 175. 1788 = *Fabricia laevigata* Gaertn., l.c. = **Leptospermum laevigatum** F. Muell., Ann. Rep. 22. 1858; et Fragm. Phytogr. Austr. **4:** 60. 1864. Native of Australia.
12. PHILADELPHUS LANIGER Ait., Hort. Kew. ed. 1, **2:** 156. 1789 = **Leptospermum pubescens** Lam., Encyc. **3:** 466. 1791. A native of Australia.
13. PHILADELPHUS LATVICUS (*P. latifolius* × *P. microphyllus*) Pochlaks & Zamelis in Acta Horti Bot. Univ. Latv. **11–12:** 230, *pl. 2.* 1939. — Rehder, Man. Cult. Trees Shrubs ed. 2, 273. 1940; et Bibl. Cult. Trees Shrubs 194. 1949. — *Nom. nud.*
14. PHILADELPHUS LODDIGESIANUS Koehne in Gartenfl. **45:** 562. 1896. — Schneider, Ill. Handb. Laubh. **1:** 371. 1905. According to Koehne's description this species has dark brown bark, ovate-lanceolate, acuminate, dentate leaves, and one, three, or five flowers with glabrous or sparsely pubescent hypanthia. Schneider remarked that this binomial represented a hybrid of unknown origin, and he doubted that it was still in cultivation in 1905.

15. PHILADELPHUS MALTAE (*P. purpurascens* × *P. coronarius aureus*) Pochlaks & Zamelis in Acta Horti Bot. Univ. Latv. **11–12:** 230. 1939, *nom. nud.*

16. PHILADELPHUS MELDERI (*P. magdalenae* × *P. schrenkii*) Pochlaks & Zamelis, l.c. *nom. nud.*

17. PHILADELPHUS MYRTIFOLIUS Soland. ex Gaertn., Fruct. Sem. Pl. **1:** 175. 1788 = *Fabricia myrtifolia* Gaertn., l.c., *t. 35, fig. 4* = **Leptospermum fabricia** Benth., Fl. Austral. **3:** 102. 1867. A native of Australia.

18. PHILADELPHUS SCOPARIUS Ait., Hort. Kew. ed. 1, **2:** 156. 1789 = **Leptospermum scoparium** Forst., Char. Gen. Pl. *72, t. 36.* 1776. A native of New Zealand.

19. PHILADELPHUS SKUJAE (*P. acuminatus* × *P. schrenkii*) Pochlaks & Zamelis in Acta Horti Bot. Univ. Latv. **11–12:** 231. 1939, *nom. nud.*

20. PHILADELPHUS SQUARROSUM Soland. ex Gaertn., Fruct. Sem. Pl. **1:** 174. 1788 = *Leptospermum squarrosum* Gaertn., l.c. *t. 35, fig. 3* = **L. scoparium** Forst., l.c.

21. PHILADELPHUS STAMINEUS Wall., Pl. As. Rar. **2:** 82. 1831 = **Deutzia staminea** R. Br. ex Wall. Num. List 3651. 1829; et Pl. As. Rar. **2:** 82, *t. 191.* 1831.

22. PHILADELPHUS TAUJAE (*P. lewisii* × *P. latifolius*) Pochlaks & Zamelis in Acta Horti Bot. Univ. Latv. **11–12:** 230. 1939, *nom. nud.*

23. PHILADELPHUS TREBOUXII (*P. falconeri* × *P. latifolius*) Pochlaks & Zamelis, l.c., *nom. nud.*

24. PHILADELPHUS VEGII (*P. falconeri* × *P. lewisii*) Pochlaks & Zamelis, l.c., *nom. nud.*

25. PHILADELPHUS "Cole Glorious" Wyman, Shrubs Vines 226. 1949 = *P. intectus* Beadle in Biltm. Bot. Stud. **1:** 160. 1902.

26. PHILADELPHUS LEWISII var. PARVIFOLIUS S. Y. Hu in Jour. Arnold Arb. **36:** 77. 1955, non Torrey = **Philadelphus lewisii** var. **pygmaeus,** *nom. nov.*

27. PHILADELPHUS LEWISII var. PLATYPHYLLUS (Rydb.), S. Y. Hu, op. cit. 78. = **P. lewisii** var. **platyphyllus** (Rydb.) A. H. Moore in Rhodora **16:** 77. 1914.

28. PHILADELPHUS SERICANTHUS var. ROCKII Koehne — S. Y. Hu, op. cit. 343, should read **P. sericanthus** var. **bockii.**

ARNOLD ARBORETUM,
HARVARD UNIVERSITY.

EXPLANATION OF PLATES V AND VI

PLATE V

REPRESENTATIVES OF THE POECILOSTIGMA SECTION, THE HABIT SKETCHES × ½, AND THE STIGMAS, STYLES AND DISCS × 2½. 1. *P. affinis* (Pringle 8833) with fruit × ½ (Moore 3238). 2. *P. myrtoides* (Calderon 687) with pubescent style and cristate stigmas (Standley 82517). 3. *P. austromexicanus* (Ghiesbreght 813). 4. *P. mexicanus* (Schiede) with fruit × 1. 5. *P. pueblanus* (Nicolas 171). 6. *P. glabripetalus* (Pringle 6311).

PLATE VI

REPRESENTATIVES OF THE SECTIONS COULTERIANUS AND STENOSTIGMA, THE HABIT SKETCHES × ½, AND THE STIGMAS, STYLES AND DISCS × 2½. 1. *P. coulteri* with pubescent style and disc (Coulter 77). 2. *P. oblongifolius* with elongated pubescent style (Purpus 5368B), the hairs with glandular thickened bases (× 20). 3. *P. osmanthus* with very short style (Chase 7310), the fruit × 1. 4. *P. pringlei* (Pringle 10174). 5. *P. sargentianus* (Sargent in 1887, fruit from Pringle 2094). 6. *P. calcicola* with united cristate stigmas and glabrous style. (Meyer & Rogers 2662). 7. *P. coronarius* with the longitudinal section of a fruit (× 2½, Sargent, July 9, 1903). 7a. Seed of *P. caucasicus*. 8. *P. pekinensis* (Hers 2515). 9. *P. tomentosus* with split stigmatic surfaces (Osmanton 382).

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A MONOGRAPHIC STUDY OF THE WEST INDIAN SPECIES OF PHYLLANTHUS *

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PHYLLANTHUS, among the subfamily Phyllanthoideae of the Euphorbiaceae, is at once the largest (650 species) and most diversified genus; it includes plants of a great many types of growth form, such as trees, shrubs, annual and perennial herbs, and floating aquatics. Although a number of species grow in dry habitats, none is at home in extreme deserts, whereas many prefer mesophytic or even hydrophytic environments. These ecological characteristics, and the inability of all except two or three species to endure cool conditions such as those in the eastern temperate United States, limit the distribution of the genus as a whole to those areas where tropical and reasonably humid conditions occur. Within these limits, however, the genus is circumtropical, well represented on all the continents and particularly the island groups lying off-shore.

In common with that of most other large angiospermous genera (those with more than 500 species), the present classification of *Phyllanthus* very inadequately reflects the true relationships between the subgeneric taxa. The difficulties in most of these large genera reside largely in their sheer size; a tremendous bibliographic study must be accomplished by the student before he can undertake biological studies of the organisms concerned.

The situation in *Phyllanthus*, however, differs from that in such genera as *Solanum*, *Eugenia*, and *Carex*, where a relatively stereotyped groundplan prevails throughout the entire genus. In *Phyllanthus* the difficulties incumbent on the great size of the group are aggravated by the fact that there are profound differences in the vegetative structure, flowers, and fruits. Some of these may be accounted for by the fact that *Phyllanthus* in its current circumscription is not an entirely natural genus; but even after the discordant groups are removed, *Phyllanthus* still remains — when vegetative and reproductive organs are considered together — perhaps the most diversified of all the great genera of the Angiosperms. The investigation of its classification and evolution should be carried out with the view of attempting to explain how this great diversity can be reconciled with the "naturalness" of the greater portion of the genus.

* Studies of the Euphorbiaceae, Phyllanthoideae, III.

The present study of the West Indian species of *Phyllanthus*, which has occupied about four years of work, is intended as the first installment of and theoretical basis for a world-wide monograph of the genus. Analysis of some 3,000 herbarium specimens of West Indian species has been supplemented by the study of specimens of many extra-Caribbean species, as well as by three field trips: to Cuba in 1951 and 1953, and to Jamaica in 1954. Of the ninety-odd species accepted in this treatment, 39 have been seen in the living condition. The lack of field work in Hispaniola has been the most keenly felt deficiency, for the species of sections *Cyclanthera* and *Phyllanthus* on that island cannot be satisfactorily understood from the herbarium specimens at hand. Since it seems impractical, however, to delay publication indefinitely in the hope of improving the treatment of these few species, their critical appraisal will be deferred to a future paper.

The eighty-odd native West Indian species of *Phyllanthus* constitute a fascinating assemblage of forms. Adapted to many different habitats and evidencing origin from various ancestral types, they exemplify well the flourishing of an evolutionarily successful group of angiosperms in the insular environment of the Caribbean. It is the main purpose of this work to attempt to capture on paper something corresponding to the biological reality of these plants as they occur today in populations on the West Indian islands, and to indicate what significance this may have for students of the West Indian flora in particular and the evolution of the angiosperms in general.

The results of these studies on the West Indian species of *Phyllanthus* will be presented in three parts: (1) a general section including historical reviews and observations on morphology and anatomy, (2) a systematic section enumerating and describing the taxa, and (3) a concluding section presenting a synthesis of all the data and discussing geographical distribution and evolution within the genus.

HISTORICAL REVIEW

The summary of the taxonomic history of *Phyllanthus* presented here centers mainly around the development of generic concepts in the subtribe Phyllanthinae as defined by Pax (1890), particularly as this applies to the species represented in the West Indies. In a previous paper (Webster, 1956), the history of *Phyllanthus* as it pertains to the American species described by Linnaeus has been discussed, including many nomenclatural details which will be omitted in the following account.

As will be shown in the section on growth form, most of the genera of the subtribe Phyllanthinae of the Phyllantheae share a peculiarity of ramification (viz., phyllanthoid branching) which gives them a similar aspect; only the less-evolved species of *Phyllanthus* itself form an exception. Although a critical understanding of phyllanthoid branching has been surprisingly slow in forming, a crude intuitive awareness of it has, since a few species first became familiar to Western botanists in the latter half of the seventeenth century, resulted in the taxa of the Phyllanthinae being treated

more or less together. In the consideration of the taxonomic history of *Phyllanthus*, therefore, it appears most practical to follow together the development of the morphological and generic concepts.

Because of its tropical and entirely non-European distribution, *Phyllanthus* appears to have been unknown to the classical authors such as Theophrastus and Pliny. Bauhin (1623) listed only a single species which would now be placed in the genus; his *Myrobalanus emblica* became the *Phyllanthus emblica* of Linnaeus. Apparently *P. emblica* was introduced into the Mediterranean area by the Arabs, in whose writings the plant is first mentioned; but for several hundred years it was known only from the fruit, which was a medicinal item.

The scientific literature of *Phyllanthus* begins abruptly in the late seventeenth century with publications by Breynius (1678) and Rheede tot Draakestein (1679), both on plants from India. Breynius's *Frutex indicus baccifer &c.* appears to represent *P. reticulatus* Poir., and Rheede's *Niruri* may be the same species. It is interesting to note that although a number of Phyllanthinae were described in various volumes of Rheede's work, the affinities between the herbaceous and woody species were not recognized. Thus, for example, *P. emblica* L. was called *Nili-camarum* while *P. urinaria* was called *Tsieru-Kirganeli.*

Hermann (1689) and Sloane (1696) opened the study of the New World species with descriptions of two species of sect. *Xylophylla*, which quickly became well-known because of their apparently anomalous production of marginal flowers on the leaves. The significance of Hermann's plant, *Phyllanthos americana planta &c.*, is that it was the basis for the name which Linnaeus applied to the entire genus. Commelin (1697) illustrated and described what was probably the same plant as Hermann's; the plate is good and easily recognizable as *P. epiphyllanthus*. Plukenet, in his "Phytographia" (1691–1696) described several species of *Phyllanthus* under various names but contributed nothing significant.

In the early part of the eighteenth century, most of the Phyllanthinae were described under two names: *Niruri* for the groups with branchlets resembling pinnate leaves (including species of *Breynia* and *Sauropus* as well as some of *Phyllanthus*), and *Phyllanthus* for the phylloclade-bearing species of *Phyllanthus* sect. *Xylophylla*. Linnaeus, in the first edition of the "Genera Plantarum" (1737), gave Dillenius the credit for first appreciating the fact that *Niruri* and *Phyllanthus* are congeneric. This insight of Dillenius represented the first important step in the development of the modern concept of the genus. He saw that in both *Niruri* and *Phyllanthus* the flowers were borne on apparent leaves, and that these leaf-like structures were homologous: in *Niruri* the flowers occurring in the axils of the leaflets of a pinnately compound "leaf"; in *Phyllanthus* (sensu Commelin), in notches on the margins of an undivided "leaf." Linnaeus, Dillenius, and their contemporaries all erred, however, in assuming that these homologous flower-bearing structures were leaves. As will be shown later this pseudo-foliar modification of the branches is one of the most important characters in defining the *Phyllanthus*-complex, even though in the present

interpretation it comes closer to characterizing the entire subtribe Phyllanthinae than it does the genus *Phyllanthus* alone.

Linnaeus in the "Hortus Cliffortianus" (1738) included in *Phyllanthus* three species, which became in 1753 *P. epiphyllanthus*, *P. niruri*, and *P. grandifolius*. The inclusion of these three very different plants — a phylloclade-bearing shrub, an herb with phyllanthoid branching, and a tree with non-phyllanthoid branching — thus established the genus at the very beginning as one with great diversity in growth form. The next important modification in the generic concept came in Linnaeus's "Flora Zeylanica" (1747) in which the *Myrobalanus emblica* of Bauhin et al. was for the first time associated with the other species of *Phyllanthus*. In the first edition of the "Species Plantarum" (1753) Linnaeus made no important modification, merely adding one new species, *P. maderaspatensis* L.: although this species belongs to a yet different section from the others, its inclusion caused no important change in generic concept.

Linnaeus's next significant contribution, in the "Mantissa" (1767), was the publication of the new genus *Cicca*, characterized by tetramerous flowers. Although he placed it in the Monoecia Tetrandria, he observed that it was related to *Phyllanthus*. Subsequently, no one has doubted the clear affinity of *Cicca* to the other species of *Phyllanthus*; the only difference of opinion has revolved around whether it merits generic or only subgeneric rank.

Four years later, in the "Mantissa Altera," Linnaeus established another new genus, *Xylophylla*, by splitting off *P. epiphyllanthus* from the other species. The new generic name was derived from the *Xylophyllos ceramica* of Rumphius, which Linnaeus renamed *Xylophylla longifolia*. The Rumphian plant, however, although it furnished the generic name, was poorly known and the genus was definitely based on the treatment of two Jamaican species of *Phyllanthus* by Patrick Browne. As indicated in a recent paper (Webster, 1956), Linnaeus and other writers were misled by Browne's erroneous description into thinking that *Xylophylla* had hermaphrodite flowers. It was purely on the basis of this fallacious character, and not upon the phylloclade-bearing habit, that Linnaeus recognized the genus; Swartz finally equated the genera in his "Flora Indiae Occidentalis" (1800), but together with Poiret (1804) and Willdenow (1809) still regarded the flowers as hermaphrodite. The confusion was at last cleared up in 1824 by Adrien de Jussieu, who retained *Xylophylla* but noted "vix a *Phyllantho* diversum." Since *Xylophylla* was merged with *Phyllanthus* by Baillon (1858) and Mueller Argoviensis (1866), relatively few authors have chosen to take it up as a distinct genus, although L. H. Bailey has recently upheld it in his "Manual of Cultivated Plants."

The most important of the post-Linnaean genera of Phyllanthinae is undoubtedly *Glochidion*, established by Forster in 1776. The absence of a disk, the characteristic androecium, and the plurilocular ovary with undivided styles all made this a very distinctive group, and it was generally maintained until Mueller Argoviensis (1865, 1866) merged it with *Phyllanthus*. This interpretation was accepted by Bentham in the "Genera

Plantarum" (1880) but reversed by Hooker in the "Flora of British India" (1887). Hooker's judgment was accepted by Pax (1890) and Pax and Hoffman (1931), as well as by most modern authors. Croizat (1943) has upheld *Glochidion* and remarked that it may be upheld "only with the understanding that its species form a natural group that it is not possible to define with reference to a set of conventional characters." This appears rather too pessimistic, however, as it actually is possible to define *Glochidion* on the basis of characters as satisfactory as any in the Phyllanthoideae.

A. L. de Jussieu, in his "Genera Plantarum" (1789), accepted *Cicca*, *Phyllanthus*, and *Xylophylla*, and added a new genus *Kirganelia* based on a Mauritian plant collected by Commerson. *Kirganelia* was distinguished on the basis of its baccate fruit and androecium of five unequally united stamens; although a distinctive group, it has generally been placed in the subgeneric rank under *Phyllanthus*. Jussieu also suggested that *P. emblica* L. might be put in a distinct genus. This was promptly done by Gaertner (1791), who placed the plant in the new genus *Emblica* as *E. officinalis*.

Olaf Swartz, in a series of publications (1788, 1791, 1800) gave the first critical treatment of the West Indian species, carefully distinguishing the Jamaican species of sect. *Xylophylla* and adding several other species. He furthermore established a new genus *Epistylium*, based on two Jamaican plants, which in more recent times has always been accepted as a section of *Phyllanthus*.

The first publication on the Euphorbiaceae which may be regarded as monographic is Adrien de Jussieu's "De Euphorbiacearum Generibus Tentamen" (1824), where for the first time all the previously published genera are critically compared and described. Jussieu accepted eleven genera of Phyllanthinae: *Epistylium*, *Gynoon*, *Glochidion*, *Anisonema*, *Agyneia*, *Cicca*, *Emblica*, *Kirganelia*, *Phyllanthus*, *Xylophylla*, and *Menarda*. This suggests an excessively narrow generic concept, but Jussieu indicates in parenthetical comments that one could just as well unite with *Phyllanthus* half of these genera: *Xylophylla*, *Emblica*, *Kirganelia*, *Cicca*, *Menarda*, and *Agyneia*. The resulting classification, with the exceptions of the inclusion of *Agyneia* in *Phyllanthus* and the separation of *Epistylium* from it, would correspond closely to the limits accepted in this treatment, and indicates that Jussieu had a good appreciation of natural affinities.

The next major revision of the Euphorbiaceae is that of Baillon (1858). Here fifteen genera of *Phyllanthus*-complex are accepted; *Emblica*, *Xylophylla*, *Gynoon* and *Anisonema* are reduced to synonymy, but *Williamia*, *Asterandra*, *Orbicularia*, *Zygospermum*, *Melanthesa*, *Sauropus*, and *Glochidionopsis* are recognized. This treatment is the last one on a world-wide scale in which there is extensive fragmentation of the group originally circumscribed by Linnaeus as the genus *Phyllanthus*. In 1860 Baillon began the publication of a "Monographie des *Phyllanthus*," but shelved it after the writings of Mueller Argoviensis began to appear in 1863. In Baillon's unfinished monograph the genus has the same delimitation as in the 1858 work; but later Baillon adopted Mueller's very broad circumscription of the genus.

Contemporary with Baillon's work was that of Grisebach, of special interest since it deals with West Indian species. In the "Flora of the British West Indian Islands" (1859), he reduced *Epistylium*, *Anisonema*, and Baillon's *Orbicularia* to sections of *Phyllanthus*, but maintained *Cicca* as distinct. Grisebach, both in "Plantae Wrightianae" (1860) and in 1865, described several new species from Cuba and one additional new section, *Williamiandra*. Grisebach's work was not especially profound and he made some serious errors in distinguishing taxa and in suggesting relationships.

Overlapping the studies of Baillon and Grisebach are those of Jean Mueller of Argau (Mueller Argoviensis), who, between 1863 and 1866 published several papers on the Euphorbiaceae, culminating in the monographic treatment of the family in De Candolle's "Prodromus." This monograph begins a new era in the study of Phyllanthinae, for not only are all of the generic concepts proposed by various authors evaluated, but also the individual species are painstakingly and accurately described, with meticulous citation of synonymy and specimens. The few flaws in execution are far outweighed by the brilliant scholarship of the treatment, which is the more striking in being perhaps the most massive critical monograph of a plant family ever accomplished by a single individual.

At first, in his long paper in "Linnaea" (1863), Mueller accepted *Glochidion* as a genus distinct from *Phyllanthus*, distinguishing it on the basis of its unbranched styles, which equal in number the cells of the ovary. By 1865 he had changed his mind, and in the revision in the "Prodromus" *Glochidion*, along with many other segregate genera accepted by Baillon, was included in *Phyllanthus*. The genus *Phyllanthus* in the inclusive sense of Mueller was thus extremely heterogeneous, comprising no less than 44 sections. In the "Flora Brasiliensis" (1873) Mueller proposed a few new sections and species but made no important modifications.

Among the post-Linnaean work on the genus, that of Mueller stands preëminent and has exercised the strongest influence in the development of the generic concept. His monograph is still the basic reference source for any taxonomic study of the genus; and although various authors compiling regional floras have resurrected segregate genera or even proposed new ones, the generally prevailing concept of *Phyllanthus* owes its circumscription to Mueller.

Impressive as was Mueller's work, it did not go unchallenged by his contemporaries. Baillon (1873) sharply criticized Mueller's treatment for its lack of appreciation of general affinities. Many of Baillon's criticisms were certainly justified; nevertheless in his "Histoire des Plantes" (1874) he accepted precisely the same generic limits as those proposed by Mueller. Bentham (1878) contributed a very interesting paper, based on his research in preparation for the treatment of the Euphorbiaceae in the "Genera Plantarum," in which he evaluated the work of Baillon and of Mueller, and made some pertinent suggestions as to affinities. He accepted Mueller's delimitation of the genus, but grouped the sections into eleven "primary sections" which correspond roughly to the subgenera of the pres-

ent treatment. This arrangement was formally presented with synonymy in the "Genera Plantarum" (1880).

The only important modification of Mueller's generic concept was made by J. D. Hooker (1887), who restored *Glochidion* to the rank of a separate genus. His remarks are interesting enough to be quoted:

"I find it inexpedient to follow Mueller (in DC. Prodr. xv. ii. 278) and Bentham (Gen. Plant. iii. 272) in reducing *Glochidion* to a section of *Phyllanthus*, from which it differs in the total absence of a disk, in habit, and in the singular modification of its styles and stigmas. Further, by keeping it distinct I comply with the wishes of the Indian Botanists, whose opinion it is of importance to consult in regard to the nomenclature of so very large and universally distributed an Indian genus."

Pax (1890) adopted the generic limits as modified by Hooker, separating *Glochidion* from *Phyllanthus* but retaining both genera in the subtribe Phyllanthinae. In the second edition of the "Naturlichen Pflanzenfamilien" (1931) Pax and Hoffman transferred several sections of *Phyllanthus*, including *Hemiphyllanthus*, *Ciccastrum*, and the New Caledonian members of the *Gomphidium*-complex, to *Glochidion*. This was a step backward, for the 1890 arrangement appears to be closer to natural affinity. Croizat (1943) has rightly objected to the extension of the range of *Glochidion* to the New World, for the genus actually appears to be confined to Asia and Australasia. The various species from South America and Madagascar which have from time to time been placed in *Glochidion* seem best retained in *Phyllanthus*, even though they do belong to a primitive group that perhaps has some affinities with *Glochidion*.

Except for the work of Pax and Hoffman, there have been no comprehensive treatments of *Phyllanthus* in the twentieth century. There are, however, two "regional monographs" which merit special mention. C. B. Robinson (1909) published a revision of the Philippine Phyllanthinae which shows observation and originality. On the basis of its drupaceous fruit, he resurrected *Cicca* as a genus distinct from *Phyllanthus* (with which it had been combined by Mueller). Baillon (1858), although also maintaining *Cicca* as a distinct genus, had remarked that the fleshiness of the fruit is not a dependable character, since there is within *Phyllanthus* a nearly continuous gradation from dry capsules to drupes. In many species the fruit is quite fleshy until late in development, when it suddenly dries out and becomes capsular. This consideration probably influenced Mueller in his reduction of *Cicca* to *Phyllanthus* (1863). As Robinson's description indicates, however, the fruit of *Cicca* is actually more distinctive than other fleshy fruits of species of *Phyllanthus*:

". . . fleshy externally, containing a 6- or 8-grooved bony endocarp, firmly united, and not separable by pressure, showing however by traces of the original carpellary walls on its exterior that it represents either 3 or 4 carpels, and containing 3 or 4 cells each with one seed."

A number of species of *Phyllanthus* have baccate or subbaccate fruits, and *P. emblica* has a drupe-like fruit resembling that of *Cicca*. But al-

though the endocarp of *P. emblica* is bony, it still separates into three cocci at maturity. The drupe of *Cicca* therefore is a good distinguishing character, as are the tetramerous flowers with the occasional production of staminodes in the females. Nevertheless, the pollen grains, seeds, and growth form are all quite typical for *Phyllanthus*. We have here a group which is on the borderline of generic status, and, despite all that has been written, one whose disposition — in our present state of knowledge — must be largely a matter of taste. *Cicca* is here retained as a subgenus of *Phyllanthus*, with the reservation however that additional study may perhaps justify Robinson's giving it generic status.

Leandri, in a considerable number of publications, has reviewed the Phyllantheae of Madagascar, where many interesting species occur. He upholds *Glochidion* and assigns several Madagascarian species to the genus, but retains *Cicca* as a section of *Phyllanthus*. The species placed by him in *Glochidion* do, like those of sect. *Microglochidion* in South America, have flowers and leaves quite suggestive of some New Caledonian species placed in *Glochidion* by Pax and Hoffman. But all these species, though forming a distinctive group and perhaps representing the ancestral form from which *Glochidion* was derived, appear best retained within *Phyllanthus*.

To conclude this survey, we have to review the concepts of those who have written on the West Indian species of *Phyllanthus* in particular. After Swartz, the first work of any importance was that of A. Richard (1850), who described some Cuban species. Grisebach, both in the "Flora of the West Indian Islands" (1859) and "Catalogus Florae Cubenses" (1866), recognized *Cicca* as distinct from *Phyllanthus*, but agreed with Mueller in relegating *Xylophylla* and several other groups to sectional rank. Wright (Flora Cubana. 1870) accepted the reduction of *Cicca* and described a few new species. Urban, in a long series of publications (1899–1930), described many species of *Phyllanthus* and often gave suggestions as to affinities. Although he published no keys or general discussions, his scattered comments are often quite to the point. Urban delimited *Phyllanthus* in the Muellerian sense, in marked contrast to N. L. Britton, who adopted a very radical conception of generic limits. The latter described from Cuba (1920) three new segregate genera — *Ramsdenia*, *Roigia*, and *Dimorphocladium* — and also recognized as genera *Conami* and *Orbicularia*. All of these, in the present treatment, are placed under *Phyllanthus*, and all except *Conami* in sect. *Orbicularia*. In Britton and Wilson's flora of Puerto Rico (1924) the species of *Phyllanthus* sensu Mueller are distributed among *Asterandra*, *Cicca*, *Conami*, *Margaritaria*, *Phyllanthus*, and *Xylophylla*; of these, only *Margaritaria* seems really generically distinct.

Recently Alain (1954) has presented a synopsis of the Cuban species of *Phyllanthus*, accepting the genus in the conservative delimitation and recognizing 65 species for the island.

When all treatments of the past seventy years are reviewed, it appears evident that the current generic concept of *Phyllanthus* is essentially that of Mueller amended by Hooker. As noted above, both Bentham and Baillon criticized Mueller's work on the basis that it did not take sufficient ac-

count of natural relationships. Bentham said of Mueller (and, with less justification, of Baillon) that he did not appear "to have sufficiently borne in mind the fact that characters differ in value in different genera or other groups. . ." Mueller, as Briquet (1896) pointed out, was an anti-evolutionist and had at first been interested in mathematics as much as in botany. Both these indications of his temperament are clearly reflected in his publications. His monograph in the "Prodromus," including keenly written descriptions of over 2,000 species in more than 1,000 species of text, is one of the triumphs of the descriptive method. But for the modern student it has a distinctly typological caste, i.e., "natural affinity" for Mueller does not appear to necessarily imply specific genetic kinship but is rather the expression of ideal relationships between mathematically definable entities. The Muellerian genus is, at least to some extent, a kind of Platonic idea of which the species are the earthly manifestations.

Nevertheless, in spite of their reservations as to Mueller's systematic criteria (and, by implication, his philosophic premises), Baillon, Bentham, and others accepted his system in the main. Although the general recognition of *Glochidion* as a genus partly altered the generic circumscription, the sections proposed by Mueller and his reductions of many groups to synonyms of *Phyllanthus* have gone largely unchallenged. This is in part due to Mueller's great authority, but also (and perhaps mostly) to the great size and unwieldiness of the genus. The present need is for a classification which will express phylogenetic relationships, and inevitably this will require drastic alterations of the Muellerian scheme. Pax and Hoffman, in the most recent (1931) general review of the genus, have — by merely adapting his system and driving the use of arbitrary characters to an even greater extreme — produced an uneven and, on the whole, unsatisfying classification.

The genera of Phyllantheae as recently maintained may aptly be compared to political boundaries which are superposed over the natural physiographic features of a region. "Phyllanthus" is the designation for all Phyllantheae in which the flowers are apetalous, lack a pistillode, and have a disk, or else do not fit into any other genus of Phyllantheae! "Glochidion" includes those plants in which the flowers are apetalous, lack both pistillode and disk, and have undivided styles. "Securinega," as Bentham pointed out, is an artificial genus in which are placed various plants related to *Phyllanthus* that have little more in common than a pistillode in the male flower.

It is apparent that not much more can be done toward constructing a new classification until a thorough morphological survey can be made of all the groups within the Phyllanthinae. Mueller, in his thoughtful critique of previous systems of the Euphorbiaceae (1866a), pointed out that one of the most glaring deficiencies of Baillon's monograph was that author's failure to study the groups beginning with the species level. It is because of this emphasis on the species as the fundamental entity that Mueller's studies are still so valuable today. Until the laborious job of analysis on this level is completed, taxonomic conclusions must necessarily be tentative,

and traditional circumscriptions of taxa accepted insofar as is possible. Nevertheless, studies already finished indicate that extensive changes, many of them nomenclatural, are immediately required, and more will be forthcoming for some time. However, it is hoped that this temporary instability in names will be compensated for by the increase in our knowledge of the biology of the organisms.

TECHNIQUES

During the course of this study, the examination of herbarium specimens and correlation of the literature have inevitably occupied a great deal of time. However, in order to advance beyond the concepts of previous workers it has been necessary to study the morphology of the plants in greater detail, using a few techniques in addition to those of standard herbarium practice. A rather sizable collection of herbarium sheets, pickled material, and seeds collected in Cuba and Jamaica has made fairly detailed investigations possible.

For analyzing the gross morphological features of herbarium specimens, a data sheet has been devised which also contains spaces to record observations on pollen morphology and leaf anatomy. Measurements of vegetative structure, fruits, and seeds were taken from dried specimens, but the flower parts (except for the calyces of female flowers) were measured in water. Refined statistical studies have not been attempted in most cases, but an effort has been made to take measurements from structures of comparable age and position. Thus, measurements of internode, stipule, and leaf blade dimensions are taken from the middle half of branchlets, unless specifically stated to the contrary. Organs abnormally developed or not fully mature have been avoided insofar as possible. However, it is not always easy to decide if a structure is fully or normally developed; unfortunately this is particularly true of the fruit and seed in *Phyllanthus*, for in some species the capsule is fleshy until late in development and in others it dehisces precociously on the drying of the specimen, whether mature or not.

The study of gross morphology presents a special problem in *Phyllanthus* because of the very small size of the flowers of many species. In many instances accurate observation requires magnifications of at least 30–50 diameters with substage lighting, and even then mistakes of observation are not precluded. In preparing dried flowers for examination, the most satisfactory method appears to be placing them in a solution of commercial photographic wetting agent; they may then be kept in small packets if reexamination is required. Commercial detergents such as "Dreft" accomplish the same end but are less satisfactory for the small-flowered species of *Phyllanthus* because they cloud the water and accumulate precipitates around the flower parts. Boiling is perfectly satisfactory for the larger flowers but is too destructive to the smallest delicate ones.

One of the chief annoyances encountered in the study of herbarium specimens was the recording of geographical data. The need for an historical

gazetteer of the West Indies becomes quite apparent to anyone who has tried to find old localities in Cuba or Hispaniola, for instance. However, Urban's bibliographic and historical notes in the "Symbolae Antillanae" (volumes 1 and 3) have helped a great deal to overcome this deficiency. For information on Cuban collectors, the summary by Leon (1918) and the discussion and map of Charles Wright's localities in Oriente Province by Jervis (1953) are especially useful. A detailed report on the explorations and collections of Ekman in Cuba and Hispaniola would certainly be appreciated by Caribbean botanists.

A better understanding of the relationships of many groups has been obtained by anatomical studies of the vegetative and reproductive structures, using the technique of cleared whole mounts as perfected by Wagner (1952) and by I. W. Bailey and his collaborators at Harvard. Individual leaves, portions of leaves, or entire flowers are first softened in potassium or sodium hydroxide for a few days; if preparations are needed quickly a few hours in heated potassium hydroxide are usually sufficient to treat even the most coriaceous leaf blades. The organs, which often are still quite opaque after this preliminary treatment, may then be bleached in 50% sodium hypochlorite until clear enough so that newsprint can be read through them. Then they are carefully rinsed in water, treated briefly in lactic acid, and stained overnight (or for a shorter period) in 50% alcoholic safranin. The tissues of most species of *Phyllanthus* appear to have a great affinity for safranin; successful preparations have been made from material left in the dye without heating for as little as thirty minutes. Following the standard method of Johansen (1940) the material is differentially destained in 95% alcohol saturated with picric acid, followed by brief immersion in 95% alcohol to which a few drops of ammonia have been added. If the material is thin, it can then be removed directly from 95% alcohol and mounted in diaphane. Very thick coriaceous leaves, however, are best transferred to absolute alcohol for a few minutes in order to reduce the chances of contamination by water. Fast green was tried as a counter-stain but proved unsatisfactory because it acted so rapidly that uniform differentiation within thick mounts was impossible. Safranin alone is perfectly satisfactory; in good preparations one can study stomata, epidermal cells, and mesophyll almost as well as the vascular strands. Foster's tannic acid method (1934) did not prove very successful with whole mounts of leaves of *Phyllanthus* because differential staining was too uneven.

No special difficulties were encountered in making microtome sections of flowers and stems and staining them with safranin and haematoxylin or fast green. Macerations of the wood of several species were also prepared to show vessel structure; these were mounted in diaphane. Free-hand sections of twigs of several species were stained with aniline blue, and slides of the species available in the Harvard wood collection were studied.

Some of the most interesting morphological data were obtained from whole mounts of pollen grains, following the technique suggested by Wodehouse (1933). The grains were squeezed on a slide by manipulation of a wetted flower and washed with 95% alcohol to remove the oil globules

adhering to them. A bit of methyl-green glycerine jelly on the tip of a dissecting needle was then touched to the grains until several of them adhered. Another clean slide was heated on a warming plate and the bit of glycerine jelly melted on it. Following the suggestion of Erdtman (1952), many mounts were prepared by placing a no. 1 circular coverslip over the jelly and running melted paraffin under the edge of the coverslip; the paraffin cools quickly and forms an air-tight seal. Continued experience, however, has shown that this method has some serious disadvantages. The paraffin seal is not durable and consequently the slides must be carefully protected and handled with great care. Furthermore, the refractive index of the glycerine jelly is not satisfactory for accurate inspection of many pollen grains. Recently, mounts have been prepared by placing the grains in lactic acid and sealing the rim of the coverslip with ordinary transparent nail-polish; exine details appear to be much clearer with slides of this type, but how long they will last remains to be seen.

Occasionally other techniques have been used to a minor extent for specific structures. Often the leaves and flowers of some species of *Phyllanthus* remain somewhat opaque even after treatment with potassium hydroxide and sodium hypochlorite. These are best studied after immersion in chloral hydrate solution for one or several days; this is particularly useful for fruits and seed coats. Microchemical tests on seed coats and leaves to determine the presence of lignin, suberin, and cellulose yielded some interesting results, and offer considerable promise for further investigations. Cytological techniques present many difficulties because of the small size of flowers and of the individual chromosomes as well as of the large numbers of chromosomes in the woody forms, but the results should be interesting enough to warrant some effort.

GROWTH FORM

As a preliminary to a detailed consideration of the morphology of vegetative and reproductive organs, the following survey of the different types of branching in *Phyllanthus* is presented.

Many of the current systematic difficulties in the Phyllanthinae are directly traceable to the lack of appreciation of vegetative structure displayed by Mueller Argoviensis. Mueller was aware of some of the differences in habit, but since he took the Linnaean view that only floral differences were of importance in defining supraspecific taxa, he only utilized the branching type to separate a few species in sections *Phyllanthus* and *Paraphyllanthus*. Nowhere did Mueller demonstrate a thorough appreciation of the significance of growth form within the genus, despite his accurate observations on minute details of floral morphology. The reason evidently lies in his lack of acquaintance with the living plants; the different types of growth form are often far from obvious with fragmentary specimens.

Hermann Dingler (1885), in his important though almost completely neglected work on the phylloclades of *Phyllanthus* sect. *Xylophylla*, was

the first (and only) author to present a comprehensive and accurate analysis of the different modifications of growth form in the genus. He not only demonstrated convincingly the derivation of the plants with phylloclades from less specialized types, but also discussed the evolution of growth form throughout the entire genus. Unfortunately, the striking results of Dingler's study were largely passed over by morphologists and systematists. In the last general review of the genus, Pax and Hoffman (1931: 61) were content to observe that the "*Viruri*-Typus" occurred in different sections; they still retained within the Muellerian sect. *Euphyllanthus* some of the vegetatively most diverse species of the genus. In the following discussion the species of *Phyllanthus* will be considered under four classes, based on the branching pattern.

Type I. As Dingler recognized, a comparatively small number of species of *Phyllanthus* have what may be termed a completely unspecialized kind of branching. *Phyllanthus polygonoides*, a widespread species of Mexico and the southwestern U.S., and its close relative, *P. platylepis* of Florida, may serve as examples of this group (PLATE-FIG. 1). Here the phyllotaxy is completely spiral and the axes are all equivalent. The only noticeable specialization is the varying length of stems and their internodes. In *P. polygonoides*, for instance, a leafy "winter rosette" analogous to that in *Panicum* subg. *Dichanthelium* is formed by shortened branches from the lowermost axils.

Many of the species in this class are vegetatively quite similar to species of *Andrachne*, but have very different apetalous flowers without pistillodes, so that the resemblance is presumably due to parallel evolution. In addition to the North American *P. polygonoides* and its relatives, several Australian species such as *P. calycinus* and *P. thymoides* have completely spiral phyllotaxy.

A number of species, both herbaceous and woody, have stems with the phyllotaxy spiralled below and distichous above. Herbaceous examples are some of the species related to the widespread Old World species *P. maderaspatensis*; the differentiation here is very slight, for the same axis may have leaves spirally arranged below and distichous above, and the inflorescences may be borne indiscriminately on any axis. These species form a transition between types I and II without, however, reducing the value of distinguishing between the classes.

Type II. In *P. caroliniensis* of sect. *Loxopodium* and *P. virgatus* of sect. *Macraea* the phyllotaxy is, at least after the first few nodes above the cotyledons, completely distichous. However, since flowers may occur at any node, there is still no differentiation of axes. Most of the representatives of this class, which includes the only really temperate species, are herbaceous, but some of the tropical species are definitely shrubs. Correlated with the distichous phyllotaxy is a trend toward more or less flattened stems with two lateral angles or wings; this line of development culminates in the Tahitian *P. aoraensis*, which has broadly winged stems similar to those in some of the tropical Loranthaceae.

Type III. A number of woody species, such as *P. grandifolius*, *P.*

nutans, and *P. pachystylus* (PLATE-FIG. 2) of sect. *Elutanthos*, present a somewhat different kind of predominantly distichous phyllotaxy. Here the seedling axis appears to bear spiral leaves, but the lateral axes all have distichous leaves except occasionally at the first few nodes on a lateral branch. In a mature, copiously branching plant of this type, the branches coming off the main stem are all alike, bearing flowers (at least potentially) at every node and producing similar branches more or less indiscriminately from the same or different nodes as the flowers.

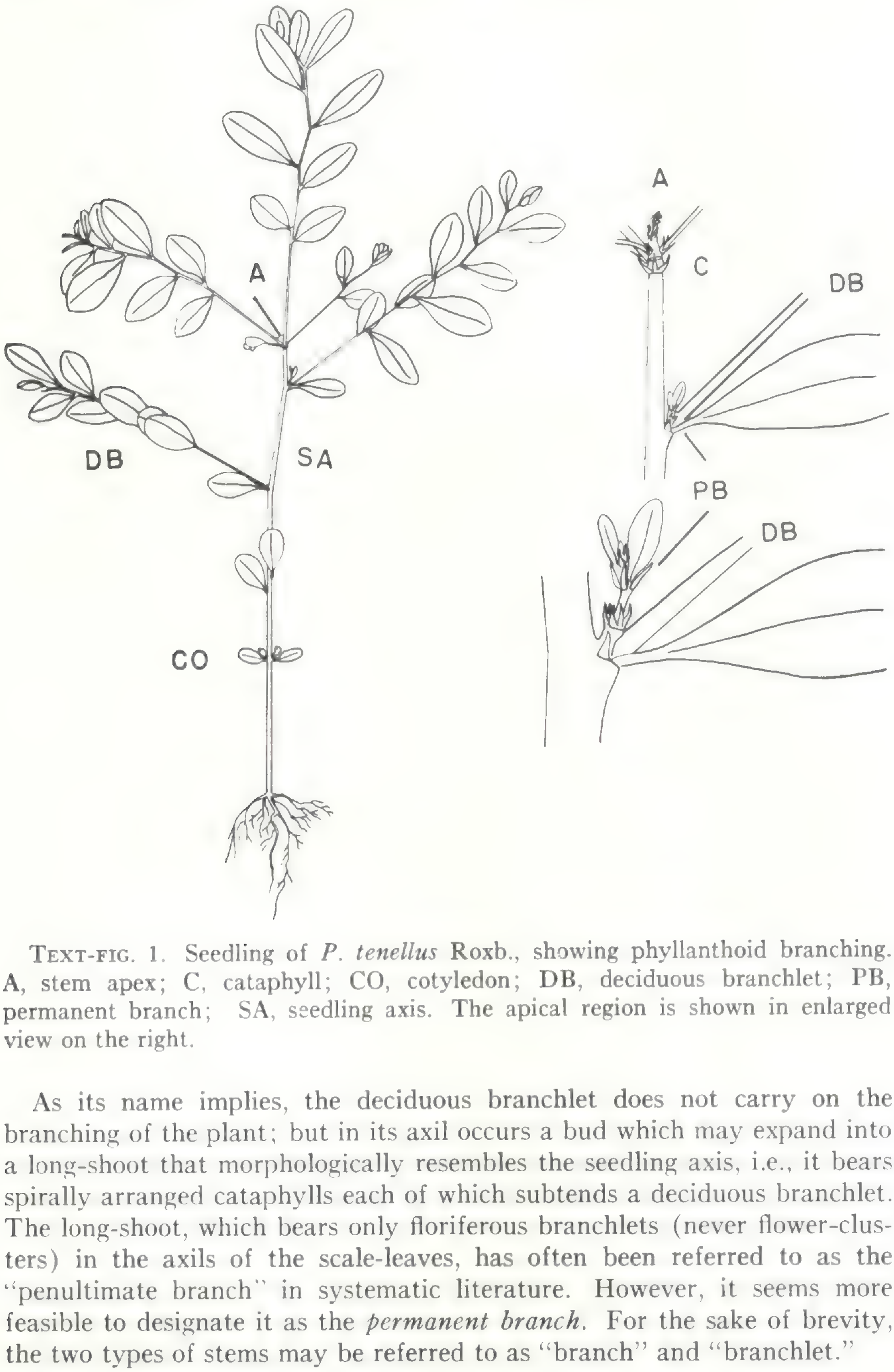
Not only is this sort of growth-form probably the most common one among tropical alternate-leaved shrubs of all families, but the same pattern of distichous-leaved lateral shoots borne by a primary axis with spiral phyllotaxy is exhibited by the seedlings of many of our familiar temperate trees such as *Celtis*, *Quercus*, *Fagus*, and *Tilia*. A common characteristic of all these plants is the persistence and essential similarity of the axes which produce flowers and new branches.

Type IV. The great majority of both the woody and herbaceous species of *Phyllanthus*, however, have a growth form radically different from those just described. In the plants of this type there are two completely different kinds of axes; the penultimate axes have spiral phyllotaxy with leaves modified as cataphylls which subtend deciduous, floriferous, distichous-leaved ultimate axes. The stems, in other words, are differentiated into persistent, flowerless, "leafless" long-shoots, and deciduous, floriferous, "leafy" short-shoots. Since this specialized type of growth form characterizes over 550 of the 650 species in the genus, it seems appropriate to designate it as *phyllanthoid branching*.

It is not surprising that among so many species there should be some unusual modifications of phyllanthoid branching. We may first profitably examine the typical situation in a species which may be clearly related to the less specialized types in the genus. As an example, a common annual weedy species, *P. tenellus* (TEXT-FIG. 1; PLATE-FIG. 3) may be useful. The seedling of *P. tenellus* usually bears normal leaves with expanded blades at the first four nodes above the cotyledons; then, however, there is an abrupt change, for the subsequent leaves on the main axis are all scale-like cataphylls. The first two lateral axes, at nodes 3 and 4, are subtended by normal leaves, but the rest are all subtended by cataphylls.

These lateral short-shoots have a very characteristic form. The proximal internode (in *P. tenellus*) is very long and the succeeding ones much shorter, so that the gross appearance of the branchlet is that of a petiolate pinnately compound leaf, and it was indeed regarded as such by the botanists of the Linnaean era. It further resembles a leaf in its limited growth and regular abscission; and in *P. amarus* and many other herbaceous species the leaves fold together along the branch-axis at night in the manner of the leaflets of a leguminous leaf. *Phyllanthus urinaria* is reported to imitate *Mimosa pudica* by responding to touch with a slow folding up of the leaves. A number of species agree with *P. tenellus* in having a distinct pulvinus at the base of the pseudo-petiole. The superficial resemblance to leguminous leaves may thus become very close indeed, but these lateral

axes of *Phyllanthus* differ, of course, in the production of flowers in the axils of most or all of the leaves. This specialized kind of short-shoot will be referred to in this work as the *deciduous branchlet*.



TEXT-FIG. 1. Seedling of *P. tenellus* Roxb., showing phyllanthoid branching. A, stem apex; C, cataphyll; CO, cotyledon; DB, deciduous branchlet; PB, permanent branch; SA, seedling axis. The apical region is shown in enlarged view on the right.

As its name implies, the deciduous branchlet does not carry on the branching of the plant; but in its axil occurs a bud which may expand into a long-shoot that morphologically resembles the seedling axis, i.e., it bears spirally arranged cataphylls each of which subtends a deciduous branchlet. The long-shoot, which bears only floriferous branchlets (never flower-clusters) in the axils of the scale-leaves, has often been referred to as the "penultimate branch" in systematic literature. However, it seems more feasible to designate it as the *permanent branch*. For the sake of brevity, the two types of stems may be referred to as "branch" and "branchlet."

Phyllanthoid branching is thus the distinctive pattern resulting from the orderly concatenation of deciduous and persistent axes. Typically, a deciduous branchlet and the bud of a permanent branch (which may or may not develop) are produced at each node on the main axis. In herbaceous species such as *P. tenellus* the branchlet and branch may appear collateral, but in woody species such as *P. discolor* the branch definitely appears to be in the axil of the branchlet. Actually, close inspection shows that even in the herbaceous species the branch arises axillary to the branchlet, although its position later shifts. The unexpanded permanent branch is therefore an accessory bud in the classical definition (cf. Gray, 1879: 44). However, Dingler (1885: 23–25), on the basis of his studies of ramification in *Phyllanthus*, advanced the theory that the permanent branch bud ("Beiknospe") is not an independent or "accessory" structure but rather represents a branch from the first node of the deciduous branchlet. He assumed that the first internode of the branchlet is so greatly shortened that the two axes appear to originate at the same level.

The spatial relationships of bracts and axes appear to support this concept. The scale which subtends the permanent branch lies obliquely opposite the cataphyll subtending the branchlet and adjacent to the main axis (TEXT-FIG. 2a). If the reverse assumption — that the branchlet is produced from the base (first node) of the branch — is made, then the latter should lie adjacent to the cataphyll subtending the branchlet rather than adjacent to the main axis (TEXT-FIG. 2b). The fact that this has never

TEXT-FIG. 2. Diagrams indicating the alternative possible positions of scales and axes at the node of a species with phyllanthoid branching. The cataphyll (C, here shown undivided for the sake of simplicity) and deciduous branchlet (DB) are shown stippled; the main stem or branch (S) and the two small axillary permanent branch buds (unlabelled) are shown lined. In the diagram on the left (2a) the scale or cataphyll (X) subtending the first permanent branch lies between the branch and main stem; this is the situation observed in living plants. In the hypothetical alternative shown in the diagram on the right (2b) the scale (X) lies on the other side of the deciduous branchlet.

been observed suggests that Dingler's idea is probably correct, so that the permanent branch may be regarded as derived from a lateral branch of the deciduous branchlet.

A further complication, however, arises with the development of the primordium of another permanent branch in the axil of the first one. Normally this second permanent branch remains arrested as a small bud but

occasionally it expands; there may even be four or five permanent branches produced at a node, each axillary to and theoretically springing from the base (lowermost node) of the one preceding. A perhaps more satisfying conception of this might be to regard the deciduous branchlet and its axillary permanent branches as a whole shoot, the lowermost branch of which has become a specialized dorsiventral structure divergent from the remaining radial branches. This would take care of a difficulty raised by the pattern of seedling development in several species. In *P. amarus* and *P. tenellus*, for example, permanent branches may occur at the cotyledonary and successive two nodes, where there are never any deciduous branchlets developed. If permanent branches are considered as ramifications of deciduous branchlets, it might be wondered how they could arise at these nodes where their "mother-axes" are missing. But on the basis of the "whole-shoot" concept, the interpretation would be that the suppression of the deciduous branchlets at the lowermost nodes, which is correlated with expanded leaf-blades, does not affect the permanent branches. It may be recalled here that the "competition" between the foliage leaf of the main axis and the leaf-like branchlet usually results in an inverse correlation of their relative development.

The systematic implications of phyllanthoid branching are nicely shown in considering the relationship between *P. tenellus* and *P. amarus*. The latter has a very similar seedling development, differing chiefly in the minor points that the first deciduous branchlet (from node 3) is sterile and that the permanent branches develop from nodes 1 and 2 much less precociously than in *P. tenellus*. Mueller placed these two species in the widely separated sections *Menarda* and *Euphyllanthus* on the basis of stamen number; but the similar growth form and pollen grains suggest that the two species are more closely related than previous taxonomic systems would suggest. Many similar instances of unnatural classification due to lack of recognition of growth forms could be adduced. On the other hand, it must be remembered that phyllanthoid branching *per se* is not necessarily an accurate guide to affinity. *Phyllanthus urinaria*, for example, has a growth form very similar to that of *P. amarus*, but it appears to be more closely related to the species of sect. *Loxopodium*, which have distichous branching. Apparently phyllanthoid branching has arisen more than once in unrelated sections of the genus, so that its taxonomic significance, though often great, must be interpreted with care.

The seedlings of *P. tenellus* and *P. amarus* have been described as having a single long-shoot, the main seedling axis, which bears the deciduous branchlets. But in older plants of these species, or ones which have been injured in some way, several of the "accessory buds" may grow out into long-shoots and the plants may thus became considerably branched. In related perennial species such as *P. abnormis* the dominance of the apical meristem is short-lived, the adult plant then developing several main branches. Among many of the herbaceous perennial species, particularly of sect. *Phyllanthus*, there is a phylogenetic trend toward loss of dominance of the apical meristem. This reaches an extreme stage in *P. pentaphyllus*,

where the primary axis becomes abortive just above the cotyledons and a cluster of wiry permanent branches grow out as coordinate main stems. The resulting habit is analogous to that in some species of *Euphorbia* subg. *Chamaesyce*, as illustrated by Croizat (1937).

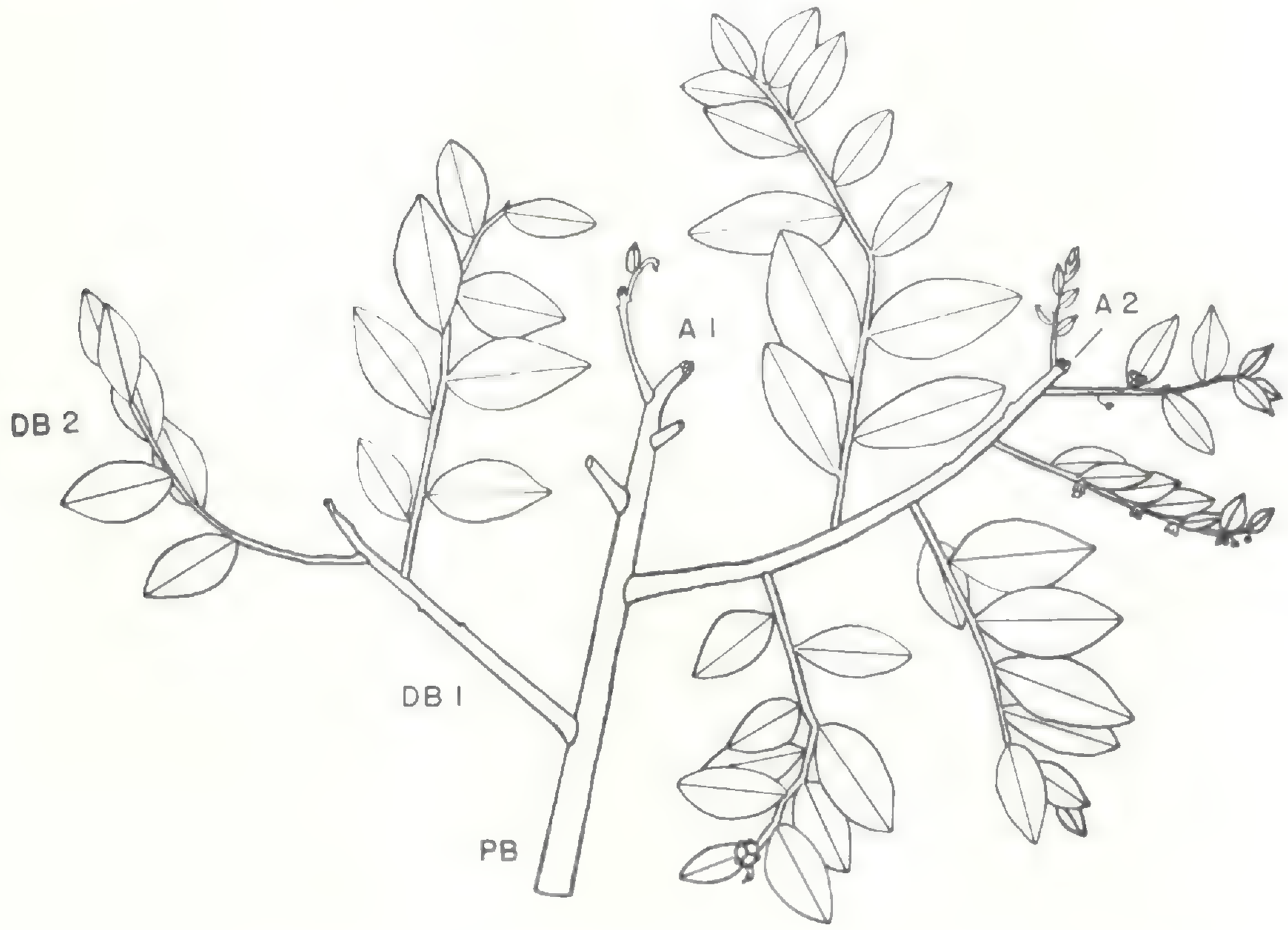
Many of the shrubby species of *Phyllanthus* probably have a growth sequence basically similar to that in *P. tenellus*, although in most cases their germination and early seedling development has not been followed. In some species such as *P. juglandifolius* of sect. *Asterandra* the permanent branches may be almost or entirely suppressed; the plants then have a palm-like or tree-fern-like ("schopfbaumartig") habit, with leafy branchlets clustered at the apex of an unbranched trunk (PLATE-FIG. 4). In other woody species, such as *P. orbicularis*, the permanent branches become well-developed and the mature plants consequently have a bushy habit.

Another complication of phyllanthoid branching is displayed by those species in which "secondary short-shoots" occur. A number of West Indian species show this phenomenon to some extent, *P. subcarnosus* being one of the best examples. Here there is superimposed on the basic pattern of permanent branch and deciduous branchlet a differential elongation of the internodes of the permanent branches. The result is that most of the current leafy branchlets will be found clustered at the tips of spur-shoots. This sort of development, which is comparable to the short-shoot development in *Gingko*, should not be confused with phyllanthoid branching, for there is no important morphological difference between long-shoot and spur-shoot.

In some species with this kind of development the spur-shoots may become so reduced that several deciduous branchlets will appear to be fascicled at the same node; the commonly cultivated *P. emblica* provides the most familiar example. In *Phyllanthus*, the cauliflorous condition appears to have arisen by a combination of extreme spur-shoot development and the differentiation of the deciduous branchlets into "leafy" sterile and "leafless" fertile axes. The result is the production of sterile leafy branches at the ends of twigs, with the flowering branchlets (the leaves often reduced to scales) developing further back at nodes from which the leafy branchlets of the previous year have fallen. *Phyllanthus emblica* has travelled part of the way toward cauliflory, for it does have fertile and sterile branchlets; but the fertile branchlets still have the leaves reduced only at the proximal end. In *P. acidus* and *P. cauliflorus* true cauliflory is achieved, but both species also produce some partially leafy fertile branchlets. In *Phyllanthus* the cauliflorous condition never reaches such an extreme state that there is no flower production by normal leafy branchlets.

So far phyllanthoid branching has been discussed with regard to those species having what may be termed "pinnatiform" branchlets, i.e., branchlets with an unramified main axis on which the leaves are attached in the manner of leaflets on the rachis of a simply pinnate leaf. But there are at least 25 or 30 species, belonging to three different sections, in which the branchlets are "bipinnatiform." In *P. ovatus* of the West Indian section *Hemiphyllanthus*, for example, the branchlet consists of a main rachis with

the leaves reduced to cataphylls but in distichous arrangement (TEXT-FIG. 3). Each cataphyll subtends a leafy floriferous lateral axis which is comparable to the entire pinnatiform branchlet of *P. amarus* or *P. jug-landifolius*, but (as shown below) not homologous with it.



TEXT-FIG. 3. Branch of *P. ovatus* Poir., a species with bipinnatiform deciduous branchlets. A 1, apex of branch; A 2, apex of primary axis of branchlet; DB 1, primary (penultimate) axis of branchlet; DB 2, secondary (ultimate) axis of branchlet; PB, permanent branch. The cataphylls subtending the ultimate axes have been omitted from the drawing.

The bipinnatiform branchlets of the species of sect. *Nothoclema* are less specialized, for normal foliage leaves are borne at all the nodes of both primary and secondary axes. In such species as *P. subglomeratus* flowers also occur at all the nodes of both axes, while in others such as *P. acuminatus* flowers may be nearly or completely confined to the lateral axes. *Phyllanthus acuminatus* has an especially interesting branching pattern: each new permanent branch (arising from the axil of a branchlet of the previous year) produces about 3–6 branchlets, the first one pinnatiform but the succeeding ones all bipinnatiform. This not only shows that pinnatiform branchlets may be derived from bipinnatiform ones by reduction, but also demonstrates that the pinnatiform branchlet is homologous to the entire bipinnatiform one rather than to one of its lateral axes.

It by no means follows, however, that pinnatiform branchlets all represent reduced bipinnatiform ones. As a matter of fact, the species with

bipinnatiform branchlets belong to rather advanced sections of the genus; and the branchlets of the species that appear to have the most primitive kind of phyllanthoid branching are all pinnatiform. These species with ramification that appears transitional between phyllanthoid and unspecialized branching are, of course, especially interesting. In *P. sellowianus* of South America and *P. gunnii* of Australia, deciduous floriferous branchlets are produced but the leaves on the main axes (permanent branches) are usually not reduced to cataphylls. This condition, which is probably primitive in these two woody species, may be simulated in specialized herbaceous species such as *P. niruri* or *P. berteroanus*, which may sometimes produce foliage leaves at all but the very highest nodes on the main axes. In this instance, however, the occurrence of unreduced leaves seems clearly correlated with the suppression of deciduous branchlets.

In all four species mentioned above the branchlets are deciduous with distichous phyllotaxy, and are the only axes bearing flowers. These are the decisive characteristics in the definition of phyllanthoid branching. The deciduous character of the branchlets should be emphasized, for the leaf-mimicking quality contingent on this feature is what gives such a distinctive aspect to the species with phyllanthoid branching. There doubtless is a correlation between the restriction of flowers to the lateral axes and their deciduous character. The evolution of phyllanthoid branching may therefore be crudely visualized to have taken place in two steps: first, the change from numerous equivalent axes with spiral phyllotaxy to a single erect main spiral-leaved stem with dorsiventral lateral branches; and second, the restriction of inflorescences to the lateral axes together with a loss of the capacity of the axes for unlimited growth. Dingler (1885: 87) visualized the predominance of the main axis over the laterals, which is a necessary prerequisite to the origin of phyllanthoid branching, as a result of the adaptation of the plant to competition with other individuals. This idea is supported by ecological studies of the tropical rain-forest which have shown that there is indeed among seedlings an intense competition for the available light and a resulting selective premium on speeded-up ontogeny. Consequently phyllanthoid branching may be imagined as an adaptation largely established by the effects of seedling competition of plants of a specific constitution. The entire, relatively small, not excessively sclerified leaves of the vegetatively unspecialized species of *Phyllanthus* may thus be conceived as "pre-adapted" for the evolution of leaf-like deciduous branchlets.

Dingler (1885: 97) noticed that the vegetatively unspecialized species of *Phyllanthus* (those with spiral phyllotaxy) show a significant ecological correlation, viz., they occur in open habitats in dry regions where there is not an intense competition for light, either between individuals or between stems on the same plant. This is doubtless true, but it would be incorrect to conclude thereby that these species are necessarily the most primitive type in the genus. There is no evidence that any species with unspecialized branching has evolved by reversion from a species with phyllanthoid branching. But slightly specialized forms such as the distichous-leaved

species of sect. *Elutanthos*, which seem to have no strictly determined vegetative structure, might well have given rise to species with spiral phyllotaxy and thus seemingly more primitive growth form.

The pervasive specialization of growth form in *Phyllanthus* culminates in the species of sect. *Xylophylla*, in which the branchlets have become leafless phylloclades. Dingler, who was the first to make a thorough investigation of the phylloclade-bearing species, suggested that the South American species of *Xylophylla* sensu Mueller were derived from "zweiaxigen" ancestors (i.e., species with pinnatiform branchlets), while the West Indian species were derived from "dreiaxigen" progenitors with bipinnatiform branchlets. This suggestion of the independent origin of phylloclades within the genus, though seeming perhaps improbable at first glance, has been decisively confirmed in the present study. Unfortunately Dingler obscured his point by claiming (1885: 101, 135–136) that the five species-groups which he recognized in *Xylophylla* represented parallel lines, each originating independently from different "beblatterten" ancestors. However, it seems most probable that the phylloclade-bearing species of *Phyllanthus* originated from only two ancestral groups. The South American species, which have probably been derived from representatives of sect. *Phyllanthus* with pinnatiform branchlets, must be grouped together in sect. *Choretropsis*. Section *Xylophylla* must be restricted to the West Indian species, which have probably been derived from sect. *Hemiphyllanthus*, the members of which have bipinnatiform branchlets.

Dingler (1885: 94–95) further made the interesting conjecture that the origin of phylloclades in the West Indian species did not represent a xerophytic adaptation as it probably did in the South American ones. He suggested instead that in the *Xylophylla* group a slight alteration in environmental conditions was probably sufficient to favor increased development of the lateral axes at the expense of the leaf-blades.

The homologies of the different types of phylloclades were investigated by Dingler (1885: 18–19), who demonstrated that the simple phylloclade of *P. epiphyllanthus* (TEXT-FIG. 4) has been derived by reduction from the compound one of some species such as *P. latifolius* or *P. speciosus* (= *P. arbuscula*) (TEXT-FIG. 5). Part of his supporting evidence was the observation that *P. epiphyllanthus* occasionally produces compound phylloclades while *P. arbuscula* occasionally produces simple ones. His report that *P. arbuscula* bears simple phylloclades on the seedling axis which are succeeded above by compound ones has been confirmed by personal observation, in Jamaica, of seedlings of this and other related species. The suggestion that the simple phylloclade represents a "Hemmungsbildung" of the compound one is supported by this evidence and by the observed reaction of a plant of *P.* × *elongatus* to pruning. The latter normally bears compound phylloclades, but when a main branch is pruned off the first phylloclades arising on the branches from the axillary buds are simple and very similar to those of *P. epiphyllanthus*. The origin of simple phylloclades is therefore analogous to the production of reduced leaves (cataphylls) on the lower part of the shoot of many plants, or to the occurrence of the

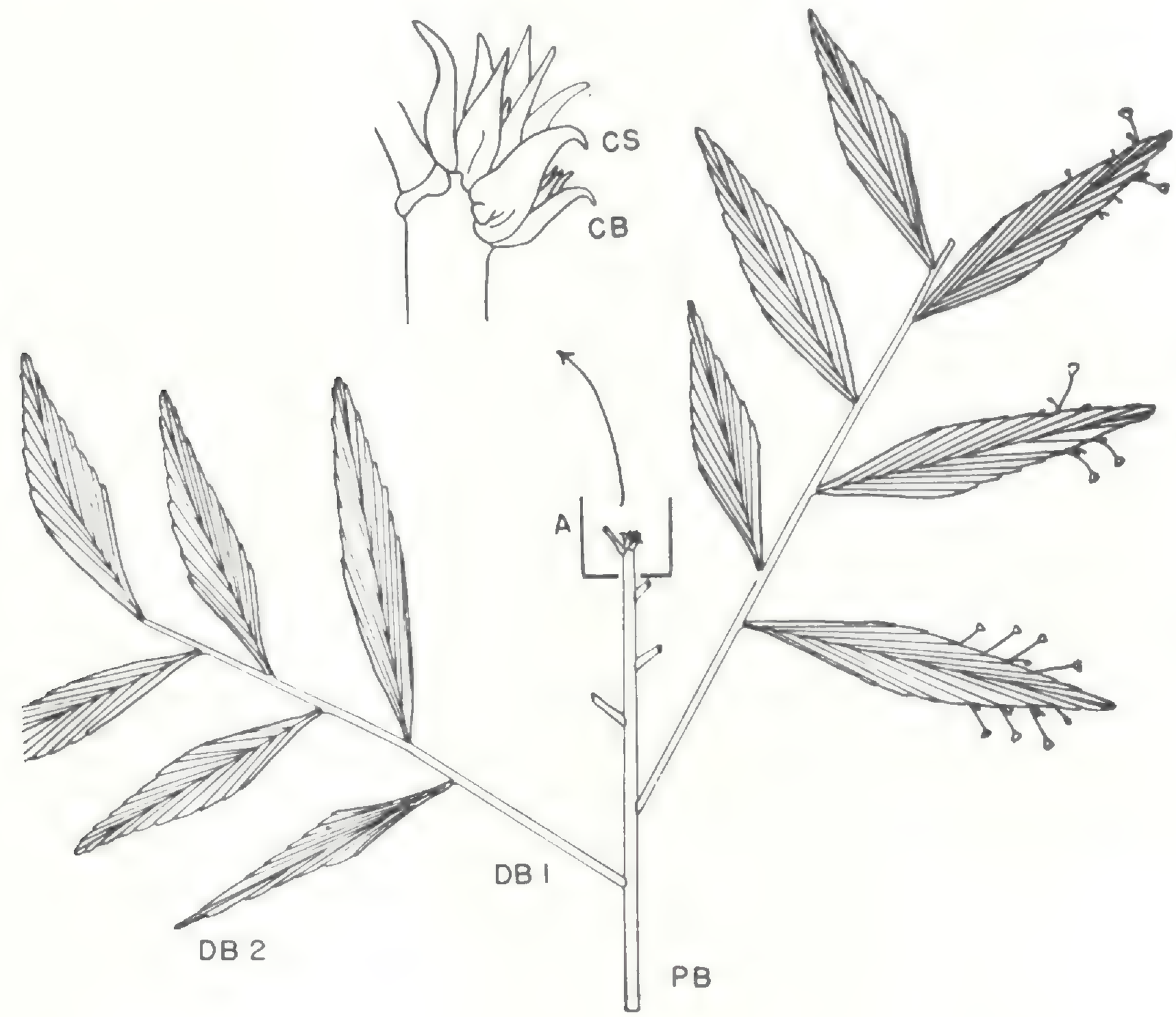
initial pinnatiform branchlet, followed by bipinnatiform ones, on the new shoot of *P. acuminatus*.

The systematic importance of phyllanthoid branching remains to be considered in its more general implications. Most, and probably all, of the species of *Breynia*, *Glochidion*, and *Sauropus* appear to have typical phyllanthoid branching; this, and evidence from floral morphology, strongly suggests that these genera are derived from *Phyllanthus* or from a closely related ancestral form. The subtribe Phyllanthinae could therefore be

TEXT-FIG. 4. Branch of *P. epiphyllanthus* L., a species with simple phylloclades. A, scaly apex (the meristem covered by aggregated cataphylls); C, cataphyll (the blade and stipules fused into a single structure in this species); DB, phylloclade; PB, branch or main stem.

characterized by phyllanthoid branching, except for the fact that a considerable number of species of *Phyllanthus* have less specialized growth forms. It is true that *Phyllanthus* as construed by Mueller and by Pax and Hoffman is polyphyletic, but even when obviously discordant groups such as *Margaritaria* are removed, there still remain over fifty species of *Phyllanthus* which have more or less unspecialized branching patterns. As will be shown later in the present study, the simple procedure of putting the species with phyllanthoid and non-phyllanthoid branching into two different genera will not work, because it obviously violates natural affinity. Not only are there close relationships between species with and without phyllanthoid branching, but it appears likely that this specialization has arisen more than once within the genus. Consequently, phyllanthoid branching, despite its importance, cannot unqualifiedly be used to define the subtribe Phyllanthinae or its constituent genera.

It is not yet clear how widespread phyllanthoid branching is among other groups of angiosperms. It has already been remarked that genera



TEXT-FIG. 5. Branch of *P. arbuscula* (Sw.) Gmel., a species with compound phylloclades. A, scaly apex, shown considerably enlarged above; CB, cataphyll blade; CS, stipule of cataphyll; DB 1, primary (penultimate) axis of phylloclade; DB 2, secondary (ultimate) axis of phylloclade; PB, branch or main stem.

such as *Celtis*, *Quercus*, *Fagus*, and *Tilia* represent a relatively unspecialized condition. The seedling of any one of these genera has a main axis bearing spirally arranged foliage leaves which subtend more or less dorsiventral lateral shoots. The leaves on the main axis are not modified into cataphylls and the ultimate branches are not ordinarily deciduous, so that these plants represent a stage equivalent to that of *P. nutans* (sect. *Elutanthos*).

There are a few temperate genera which show a closer approach to phyllanthoid branching. In both *Pinus* and *Berberis* there are long-shoots bearing spiral cataphylls which subtend short-shoots of limited growth. In *Berberis vulgaris*, as illustrated by Gray (1879: fig. 234), the long-shoot has at the base one or more nearly typical leaves, but the succeeding ones become more and more spine-like until the upper nodes bear only three-pronged spines. The chief differences from phyllanthoid branching are the gradual transition from foliage leaf to cataphyll and the presence of radial non-deciduous shoots. The leafy short-shoots of *Pinus* are much more limited in growth than those of *Berberis* but still are radial, and furthermore do not bear reproductive structures. Thus although *Pinus* and *Berberis* show a certain approach to the growth form prevalent in the Phyllanthinae, their branching patterns are not specialized enough to be classified as phyllanthoid.

So far the only plant outside of the Phyllanthinae in which phyllanthoid branching has been observed is *Casearia sylvestris* (Flacourtiaceae), living plants of which were examined in the Atkins Gardens, Soledad, Cuba. In this species the leaves on the main axis are reduced to cataphylls and the lateral axes are floriferous, leafy, deciduous branchlets; the resulting habit of the plant is quite similar to that of such species of *Phyllanthus* as *P. juglandifolius*. *Casearia*, like *Phyllanthus*, shows considerable diversity in growth form, for many species in the genus certainly have non-phyllanthoid branching. It is not impossible, of course, that phyllanthoid branching may be found in other genera of the Flacourtiaceae or in other families with tropical woody representatives. The various genera with the habit of miniature trees ("Schopfbaümchen") would be apt to exhibit approaches to or modifications of phyllanthoid branching. There are a number of interesting evolutionary problems connected with this possibility. Richards (1952: 76–77), for instance, has observed that the majority of the shrubs in the tropical rain forest have the Schopfbaum habit and has suggested that these plants should be regarded as procociously reproducing trees. This does not appear to be the case in *Phyllanthus*, but it would be interesting to investigate the problem in other families.

STEM

The morphology of both the vegetative and floral parts of *Phyllanthus* may be profitably discussed in close conjunction with their anatomy. This is particularly apropos in the Euphorbiaceae, where anatomical studies have played a systematically significant role. The family was one of the

first to be thoroughly investigated from the standpoint of correlating anatomy with systematics; Pax (1884) initiated this phase of study in the Euphorbiaceae by applying anatomical criteria to test the validity of the various suprageneric groupings proposed by Mueller, Baillon, and Bentham. Since Pax became the chief authority on the systematics of the family, an emphasis on anatomical definition of the taxa tended to be maintained.

Subsequent to Pax's classical paper, the Munich school of anatomists led by Radlkofer greatly extended the knowledge of the anatomy of the Euphorbiaceae by investigating several tribes in greater detail. The researches of most direct interest here are those of Froembling (1896), who worked with the Muellerian subtribe Euphyllantheae. He studied 87 species of *Phyllanthus* sensu Mueller; but in interpreting his results it must be remembered that about 20 of these have subsequently been removed to other genera (mostly to *Glochidion*). Rothdauscher (1896) provided a good report on the Phyllantheae other than the Euphyllantheae which summarizes data of value for anatomical comparisons of *Phyllanthus* with related genera.

Comparatively little detailed histological work has been done on the Phyllantheae in subsequent years. Gaucher (1902) presented an anatomical survey of the Euphorbiaceae which contains some information of interest. Unfortunately, however, he either ignored or was unaware of the work of the Radlkofer school, and as Solereder (1908: 1048) has pointed out, some of his reports are at variance with those of previous workers. He considered only 20 species of *Phyllanthus* and did not discuss most of them individually. Dehay (1935) has contributed an interesting monograph on the vasculation of leaf and petiole in the Euphorbiaceae which deserves to be followed up by further research. There seems little doubt that the technique of petiolar cross-sections offers considerable promise in defining some of the intrafamilial groups.

Most recently Metcalfe and Chalk, in their "Anatomy of the Dicotyledons" (1950, based on the compendium of Solereder, 1899), have summarized the anatomical information on the family. Their digest of the many papers is valuable, although their bibliography shows some notable gaps in the systematic anatomy of the Euphorbiaceae.

Despite the relatively large amount of anatomical work which has been done on the family, however, it is apparent that a comprehensive synthesis of this information with evidence from other fields such as gross morphology and cytology has not been attempted. An assimilation of what has already been accomplished is required in order to pinpoint the outstanding problems. The intensive investigation of these would then go far toward improving the classification of this large and difficult family.

The aim of the present treatment is to bring together what has specifically been published on *Phyllanthus* and to add personal observations on preparations of West Indian material. These studies have not so far shown anatomical characters to be of any great use in distinguishing closely related species, but as Pax suggested, they are of particular value in indicating affinities between groups of supraspecific rank. Here anatomical

distinctions may sometimes prove invaluable in suggesting whether certain floral characters represent true affinity or only parallel evolution. In some of the following discussions, therefore, the features observed in *Phyllanthus* will be compared with those in other genera and tribes. The root will not be given any special attention, since it does not appear to show any interesting modifications. Since the gross morphology of the stem has been discussed in the preceding section on growth form, the present consideration of the stem will center on internal characters as seen in macerations and in sections of twigs and mature wood.

Pax (1884: 413), in establishing the tribes and subfamilies of Euphorbiaceae on an anatomical basis, distinguished the Phyllanthoideae from the Crotonoideae on the basis of its lack of both intraxylary phloem and laticifers. He could distinguish the Phyllantheae from the Bridelieae, however, only on the basis of the production of secondary bast fibers in the latter and their absence in the former. Subsequent observations have in the main confirmed these diagnostic characters but have so far contributed little to the definition of the subtribes.

As a typical example of young stem structure in *Phyllanthus*, the widespread tropical shrub, *P. reticulatus* var. *glaber* may serve (PLATE-FIG. 5). Free-hand cross-sections of both branches and branchlets of this and over a dozen other species were stained in aniline blue and mounted in glycerine for study; some cleared whole-mounts of stems were also studied. The structure in *P. reticulatus* will be explained first and then the other species will be compared with it.

The nodes of *P. reticulatus* (PLATE-FIG. 6) are trilacunar with a single trace from each leaf-gap. The same structure is developed in all other species investigated, although the configuration of the traces varies somewhat depending on the size of the foliar parts. In *Phyllanthus*, as in most Euphorbiaceae, the two lateral traces supply the stipules and only the central trace enters the base of the petiole. In species such as *P. acidus*, which have small, delicate stipules the stipular traces are so small that in a slightly oblique free-hand section of the nodal region the node may appear unilacunar. In species with relatively massive stipules such as *P. maleolens*, however, the stipular traces are large and conspicuous (PLATE-FIG. 7).

The epidermis of the young stem of *P. reticulatus* is composed of small chlorophyll-less cells with slightly convex outer walls covered by a thin cuticle; rarely, occasional cells are tanniniferous. In other species, such as *P. shaferi*, *P. subcarnosus*, and *P. maleolens*, the cuticle is considerably thickened. In all species examined, the stomata are nearly plane with the surface of the epidermis, or at least are not distinctly sunken. In both the stem and branchlet of *P. reticulatus* there is a distinct hypodermis which is usually one cell thick and composed entirely of tanniniferous cells. The term "hypodermis" is here used in the noncommital topographical sense of Solereder (1908: 1076 -1077), as developmental studies are still required to establish whether it is a true hypodermis or a double epidermis which is developed in *Phyllanthus*. In *P. acidus*, *P. emblica*, and *P. discolor* there is no differentiated hypodermis, while in *P. subcarnosus* it is well-defined.

In the branchlet of *P. reticulatus* the remainder of the cortex is composed of unspecialized parenchyma cells; but in the stem, where the cortex is much thicker, there are quite a number of tanniniferous cells (some of them aligned in more or less discontinuous rows which roughly parallel the hypodermis) and the cell-layers immediately beneath the hypodermis are formed of collenchyma. Conspicuous tannin cells were also observed in the cortex of *P. emblica* and *P. maleolens*, while in the material examined of *P. subcarnosus* and *P. acidus* tannin is lacking. *Phyllanthus shaferi*, *P. incrustatus*, and *P. maleolens* have stone cells in the cortex, and the first two species have rhombic crystals as well.

In *P. reticulatus* the primary phloem ("pericycle") fibers are thin-walled and occur as near-contiguous caps separated by the phloem rays. The other species of *Phyllanthus*, and those investigated by Froembling, also had primary phloem fibers occurring in discontinuous groups, although some had elements with thicker walls. The phloem parenchyma in *P. reticulatus* stands out in cross-section because of the abundance of longitudinally elongated tanniniferous cells.

All the species investigated had relatively thin-walled primary and secondary xylem elements; and nothing was seen suggesting the condition reported by Pax (1884: 399; pl. 6, fig. 10), who claimed that the xylem nearest the pith was in the Phyllantheae composed entirely of extremely thick-walled "Tracheiden" [fibers?]. Although Pax (l.c.) qualified his statement by saying that the condition was poorly developed in a number of species of *Phyllanthus* and *Breynia*, it is probable that he was mistaken as to the nature of the cells concerned. Rothdauscher (1896) reported no such "primary" elements in his detailed examination of the Phyllantheae. Probably the cells in question are lignified pith cells, which Rothdauscher (1896: 18, 86) reported for the majority of the *Phyllantheae*, including *Hemicyclia*, the genus Pax used for his illustration.

The pith of *P. reticulatus* consists of parenchyma cells with unlignified walls; those of the branchlet appear to lack contents but those in the stem may contain crystals or tannin. Tannin was also observed in the pith in *P. abnormis*, *P. cladanthus*, and *P. emblica*. Conspicuous formation of starch in the pith was seen only in *P. acidus*. *Phyllanthus shaferi* has rhombic crystals in the pith, while *P. incrustatus* is the only species investigated showing stone cells in both pith and cortex. Lignification of the walls of the pith cells was observed only in *P. maleolens*; but in *P. discolor* and *P. montanus* the walls have a striking appearance due to the conspicuous primary pit fields. These are enlarged, more or less elongated, and may be appressed side-by-side so that the entire wall has scalariform pitting like that between vessels and ray parenchyma cells. Metcalfe and Chalk (1950: 1228) report medullary bundles in *Phyllanthus*, but examination of the West Indian material and of the literature has failed to suggest any basis for their statement.

The mature stem structure may now be surveyed, beginning with the periderm. Cork formation is mainly subepidermal, as reported by Froembling (1896: 71); the single species mentioned by him as forming cork

within the pericycle, *P. obovatus*, is really a species of *Glochidion*. Gaucher (1902: 171) found that in *P. welwitschianus* the cork cambium develops in the second or third sub-epidermal layer. *Phyllanthus incrustatus*, and a few other West Indian species, have a precocious and excessive amount of cork production which results in the breaking up of the epidermis (and perhaps one or two outer layers of the cortex) into plates; the stems of these species consequently have the curious appearance of being incrusted with bran-like flakes (PLATE-FIG. 8). Unusually specialized cells were not encountered in the cork of most species, although a few sclerenchyma cells were noted along the inner edge of the cork in *P. emblica*.

Pax (1884: 413) reported that sclerenchyma was formed only in the primary phloem in the Phyllantheae, but Froembling (1896: 71) and Rothdauscher (1896: 22) found secondary "Hartbast" present in both the Euphyllantheae and the remainder of the Phyllantheae. Froembling noted that these secondary elements, which could be distinguished from the primary ones by their different color and greater diameter, occurred in the secondary phloem of a number of species of *Phyllanthus*, including the West Indian *P. ovatus* and *P. nutans*. Among the Harvard material, secondary fibers of this sort were observed in *P. emblica*. In *Phyllanthus*, as in other genera of the Phyllantheae, this secondary phloem sclerenchyma is scanty and does not form definite layers. Whether this breaks down the supposed distinction of the Phyllantheae from the Bridelieae, which are reported to have distinct layering of parenchyma and sclerenchyma in the phloem, remains to be seen.

Stone cells were reported in the phloem of *P. multilocularis* and *P. helferi* by Froembling, but these two species actually belong in *Glochidion*. No stone cells have as yet been detected in the phloem of *Phyllanthus*, although they probably occur. Froembling also noted many small druses borne in septate fibers ("Krystalkammerfasern") in the phloem of most species of *Phyllanthus* and reported styloids in several, as well as compound ("zusammengesetzte") crystals in the form of a "W" in *P. wightianus*. In the Harvard material, styloids were observed in the chambers of elongated, septate, thick-walled cells in the phloem of *P. emblica*. But these cells, the "Krystalkammerfasern" of Froembling, are not lignified as are the septate fibers in the wood.

The structure of the xylem of *Phyllanthus* is much better known than that of the phloem. The following account is based on personal observations and on data from Froembling (1896), Janssonius (1930), Pearson and Brown (1932), and Metcalfe and Chalk (1950). The descriptive terminology is based on the standard definitions as presented by Moseley and Beeks (1955) in their comparative analysis of the xylem of the Garryaceae. An important qualification which should be kept in mind is that the majority of species of *Phyllanthus* are not truly arboreal, and many of the shrubby species have very slender stems. Consequently, the amount of secondary xylem of many species will be inadequate for comparisons between mature and young wood or between woods of different species.

The tracheary elements in the xylem of *Phyllanthus* are vessels and libriform fibres. In cross section (PLATE-FIG. 9) the vessels appear mostly solitary or in groups of two or three, although Janssonius reports radial groups of up to eight in *P. emblica*. Vessel diameter is very small. In the four species on which measurements (of one hundred for each species) were made, the range and mean diameters were found to be as follows: *P. emblica* 52–99 μ, mean 75.6 μ; *P. botryanthus* 23–58 μ, mean 40.2 μ; *P. incrustatus* 20–47.5 μ, mean 35.4 μ; and *P. orbicularis* 20–44 μ, mean 30.3 μ.

Pearson and Brown and Janssonius reported 13–25 vessels per square mm. in *P. emblica*, but in the Harvard material the average was 53 per square mm., "very numerous." Apparently this species, which has ill-defined growth rings, is quite variable in density of vessels. *Phyllanthus botryanthus*, which is believed to be a rather primitive species on the basis of its growth form, shows this anatomically in its extremely numerous small vessels which average about 97 per square mm.! Examination of additional species is desirable, in order to determine whether this high vessel density is general throughout the genus.

As reported in the literature, all species examined have vessel-elements with simple perforations, but the end-walls of the vessel-elements are usually quite oblique (PLATE-FIG. 12). Inter-vascular pitting is alternate and small, while pitting to ray or xylem parenchyma cells is simple or narrowly bordered with larger pits that are often transversely elongated or even scalariform.

As may be seen from TABLE 1, the vessel-elements of *Phyllanthus* fit neatly into the "medium-sized" class, the mean lengths falling within the 350–800 μ range. There is no apparent correlation between vessel-element length and taxonomic position, at least on the basis of the relatively few species so far investigated.

The xylem fibers of *Phyllanthus* are ordinarily septate and have very small inter-fiber pits with linear orifices (PLATE-FIG. 13). They vary in total length from about 350 μ ("very short") to about 1700 μ ("moderately long"), with the mean lengths of 700–1100 μ covering the "moderately short" range. The mean fiber length appears to be a much better indicator of degree of specialization and of systematic position than does the mean vessel-element length, but the correlation is far from exact. *P. pachystylus* and *P. microdictyus*, two of the most primitive species examined, do have long fibers averaging 992 and 1003 μ respectively, while those of the highly specialized *P. orbicularis* and *P. epiphyllanthus* average 700 and 731 μ. But *P. chryseus*, which is also a highly evolved species, has the longest fibers of the species studied, the mean falling at 1098 μ. The data as a whole, nevertheless, are suggestive enough to warrant a much more extensive survey of the lengths of imperforate tracheary elements within the genus.

Xylem parenchyma in *Phyllanthus* is mostly paratracheal and scanty, one or a few cells commonly occurring adjacent to a vessel and often between a vessel and a ray. As Pearson and Brown stated, there is also very

scanty metatracheal parenchyma in *P. emblica*, diffused among the fibers. Janssonius reports that the xylem parenchyma strands in *P. emblica* are up to six cells high, and the pit-pairs to vessel elements either simple or half-bordered.

TABLE I

LENGTH OF TRACHEARY ELEMENTS *

Species	Range of fiber length	Mean fiber length	Range of vessel element length	Mean vessel element length
P. pachystylus (Webster 3906)	577–4150 μ	992 μ	202–974 μ	477 μ
P. microdictyus (Webster 3809)	607–1480	1003	368–932	638
P. incrustatus (Webster 4014)	444–1243	993	340–1021	761
P. orbicularis (Webster 3884)	383–1406	700	281–696	474
P. epiphyllanthus (Jervis 1368)	370–1510	731	168–706	429
P. subcarnosus (Webster 4683)	400–1566	936	330–765	600
P. chryseus (Webster 3853)	661–1723	1098	296–1479	702

* All measurements are in microns, on the basis of 100 fibers measured for each species; total numbers of vessels measured varies as follows: *P. pachystylus* 100; *P. microdictyus* 40; *P. incrustatus* and *P. orbicularis* 50; *P. subcarnosus* 60; *P. chryseus* and *P. epiphyllanthus* 100.

The rays in the two species of *Phyllanthus* studied from radial and tangential sections are so different that they must be described separately. As reported by Janssonius and by Pearson and Brown, only multiseriate rays are present in the xylem of *P. emblica*. These rays in tangential section appear composed of roundish cells, with uniseriate wings absent or rudimentary. In the classification of Kribs (1935), the rays therefore fall into the category Homogeneous II (PLATE-FIG. 10). The rays in *P. botryanthus*, on the other hand, clearly belong in the class Heterogeneous IIA: the multiseriate rays have long uniseriate wings, the uniseriate rays are abundant and well-developed, and transitional forms between the two types are rare (PLATE-FIG. 11).

The rays of *P. emblica* and *P. botryanthus* differ quantitatively as well as qualitatively. The multiseriate rays of *P. emblica* are greatly elongated vertically, some of them hundreds of cells and over 5000 μ high; transversely, they are 2–9-seriate and up to 190 μ wide. These massive rays occupy such an appreciable bulk of the wood that there are only 3–5 of

them per mm. In contrast, the multiseriate rays of *P. botryanthus* are mostly only 15–40 cells high (extremes 10–80, including the wings) and 2–5-seriate, with conspicuous uniseriate wings of 5–15 cells; they are so much less bulky that there are about 14 rays per mm. (including the uniseriate). The uniseriate rays of *P. botryanthus*, which consist of vertically elongated cells quite unlike the roundish ones making up the bulk of the multiseriate rays, are mostly 4–10 cells high but sometimes up to 20. In the rays of both species are some cells containing tannin and others with rhombic crystals of calcium oxalate.

The striking differences in ray structure between these two species is an indication that further investigation within the genus might provide taxonomically significant results. Section *Emblica*, to which *P. emblica* belongs, has at various times been recognized as a genus distinct from *Phyllanthus*. The validity of this and other generic segregates may ultimately be decided partly on the basis of such evidence from wood anatomy.

The difference in the rays of *P. emblica* and *P. botryanthus* assumes additional significance when the affinities of the fossil woods assigned to the form-genus *Paraphyllanthoxylon* are considered. As established by Bailey (1924) on the basis of Cretaceous petrifactions from Arizona, the genus was characterized by scanty paratracheal parenchyma, vessel-elements with simple perforations, septate fibers, and mostly multiseriate rays with 1–5 elongated marginal cells. The rays are thus more or less intermediate between those of *P. emblica* and those of *P. botryanthus*. It is quite possible that *Paraphyllanthoxylon arizonense* belongs to one of the genera of Phyllanthinae, and it may prove to represent a species of *Phyllanthus* of an extant section when the xylem structure of the genus is better known.*

The detailed anatomy of the species of *Phyllanthus* in which the stems are modified into phylloclades will be discussed in another place, where extended analyses of individual species can be given. Here the purpose is to indicate in a general way how the phylloclades compare anatomically with the less specialized kinds of stems. As Dingler suggested, an independent evolution of phylloclades appears to have occurred in the South American and West Indian species which were all placed by Mueller in sect. *Xylophylla*. Consequently, the South American plants should be associated with *P. choretroides* in sect. *Choretropsis*, and sect. *Xylophylla* should be restricted to include only the West Indian species. Dingler also contributed the interesting suggestion that the phylloclades of the two groups could be distinguished in a general way on the basis of their respective patterns of development. In the phylloclades of sect. *Xylophylla*, it is the cortex which undergoes the most intensive growth to make up the bulk of the mature structure, while in sect. *Choretropsis* the cortex remains thin and a larger volume is occupied by the pith. A corollary of this is

* Since this paper went to press, examination of additional material (kindly loaned from the Yale slide collection by Dr. William Stern) has shown that in *P. acuminatus* the ray structure is more or less intermediate between that of *P. emblica* and *P. botryanthus*, and thus approaches *Paraphyllanthoxylon*.

that in sect. *Xylophylla* the vascular cylinder tends to break up into several closed bundles and thus produce a polystelic appearance, whereas in sect. *Choretropsis* the stele merely becomes greatly flattened.

The compound phylloclade of the commonly cultivated "greenhouse" *Phyllanthus*, *P.* × *elongatus*, shows in cross-section a structure more or less characteristic for all the species of sect. *Xylophylla*. In both the penultimate (PLATE-FIG. 14) and ultimate (PLATE-FIG. 15) axis there is a layer of chlorophyll-less hypoderm underlying the rather thickly cutinized epidermis. The outer cortex is composed of chlorenchyma which is not clearly differentiated into either palisade or spongy mesophyll, while the inner cortex resembles the pith. The numerous cortical bundles of thick-walled fibers appear mostly to be independent of the vascular tissue, as reported by Dingler (1885: 36), although they are structurally similar to the fibers of the primary phloem bundles and may sometimes be derived from these. The chief difference between the penultimate and ultimate axis is in the stele, which is intact, although flattened, in the penultimate axis but is broken up into concentric bundles in the ultimate axis so that a polystelic appearance results. The simple phylloclade of *P. epiphyllanthus* (PLATE-FIG. 16) anatomically resembles the ultimate axis of the phylloclade of *P. elongatus*.

The simple phylloclade of *P. montanus* (PLATE-FIG. 17) differs from those of the other West Indian species anatomically as well as in its more leaf-like outer form. The mesophyll is organized into a very dense palisade layer encircling the phylloclade just within the hypodermis, so that the structure appears that of a "centric" leaf-blade. But the greatest difference is in the stele, which is flattened and somewhat dissected but with the xylem masses on the abaxial and adaxial sides facing one another; no concentric bundles are formed. The phylloclade of *P. montanus* therefore resembles the penultimate axis of the phylloclade of *P. elongatus*. In this respect it resembles the phylloclades of the South American species of sect. *Choretropsis*, but this must be regarded merely as an interesting case of convergent evolution.

(*To be continued*)

THE AMAZON INDIAN AND EVOLUTION IN HEVEA AND RELATED GENERA

RICHARD EVANS SCHULTES [1]

With four plates

I.

TO-DAY the genus *Hevea* is one of the most important groups of plants to civilised man, for it is the source of an overwhelmingly large part of his natural rubber. Despite the fact that rubber is indispensable to modern civilisation, it is wholly possible that the earliest use man made of *Hevea* was merely as a source of food. Even now, the Indian who lives in the murky corners of the Amazon forest has little use indeed for the rubber-bearing latex of the tree. Nevertheless, the seeds of various species of *Hevea* are, in season, a regular and esteemed article of diet amongst many tribes of the northwest Amazon.

It is meet that a thorough study of the role of *Hevea* as a food be made. The subject is of intense ethnobotanical interest in itself, but there is yet a more compelling reason for examining this relationship between man and rubber trees. A recent series of thought-provoking articles (1, 2, 4, 10, 40, 41) implies that this curious relationship has acted as a catalytic factor in certain phases of the evolution of the genus. Far-reaching conclusions have been drawn. Some of these conclusions call for objective examination, lest they become so intricately elaborated, so confounded and so widely accepted that their critical evaluation turns out to be a much more difficult task.

In this paper, I propose 1) to review what we know of the history of the utilisation of *Hevea* as a food; 2) to discuss my own observations of this particular use of the rubber [2] tree in the northwestern part of the Amazon Basin; and 3) to evaluate the recently proposed hypotheses as to how this use may have affected evolution in *Hevea*.

There is a group of related genera in the Euphorbiaceae to which *Hevea* is usually assigned: the *Hevea-Micrandra-Vaupesia-Joannesia* complex. Forasmuch as the seeds of several species of *Micrandra* and *Vaupesia* are used by Indians in an identical way as a food, our discussion will necessarily include these genera. We would be warranted in assuming, I believe, that whatever evolutionary influence this use may have had in *Hevea*

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[2] In this paper, I use the term "rubber" or "rubber tree" to refer only to *Hevea*, and to refer to all species of Hevea, not merely the commercially important species, *H. brasiliensis*; the term *cunuri* refers to *Micrandra Spruceana*.

could be paralleled in the case of related genera growing in the same area and habitats. No discussion of *Joannesia* is needed, for its seeds have never been reported as a food.

II.

Preliminary to a discussion of any phase of evolution in these groups, a short summary of the genera in question would seem to be in order, especially so since there has been so much difference of opinion in the past in regard to their classification.

HEVEA Aublet

Described in 1775 by Aublet (3) from material collected in French Guiana, *Hevea* is by far our most important genus of rubber yielding plants. It is the source of more than ninety-five percent of the world's natural rubber, and most of this amount is produced by a single species: *Hevea brasiliensis*. The genus is native to South America, where it is

FIGURE 1. Aerial view of the forests of the Río Apaporis below the Falls of Jirijirimo, Colombia. The great massif of the Cretaceous, quartzitic Mount Isibukuri can be seen in the background. Much of the topography of the northwest Amazon (the basins of the Rio Negro and Río Caquetá) is of this rolling type with large areas which, unlike the eastern and central parts of the Amazon Valley, are never subjected to flooding. On this high, rolling hinterland the abundant species of *Hevea* are *H. guianensis*, *H. guianensis* var. *lutea*, *H. nitida*, and *H. pauciflora* var. *coriacea*.

known from the Amazon Valley, the upper Orinoco Valley, the Guianas and the Matto Grosso region of Brazil. Highly typical of the Amazonian "hylaea" (16), *Hevea* exhibits much morphological variability and chooses a wide range of ecological sites. Its members range from forest giants to shrubby, sometimes almost prostrate, treelets and are found growing in deeply flooded alluvial land, in acidic boggy sites, on high well-drained upland and on the tops of xerophytic quartzitic mountains. As in many groups of tropical trees, natural variability has led, in the past, to the description of too many specific concepts. At one time, specialists held that the genus comprised twenty or more species (18, 19, 21), but recent workers are in essential agreement that there are only eight or nine (4, 11, 13, 14, 31, 32, 33, 40, 41). Trees of *Hevea* are usually called *seringa* or *siringa* in Brazil, Colombia and Venezuela, *shiringa* or *jebe* in Peru and Bolivia.

1. **Hevea Benthamiana** Mueller-Argoviensis in Linnaea 34: 204. 1865.

An inhabitant of low alluvial flood-sites and often-times growing in all-year *Mauritia*-bogs, *Hevea Benthaniana* is one of the most distinct of the species. It occurs only north of the Amazon River in the northwestern part of the Amazon Valley and the upper Orinoco. It is especially abundant in the Rio Negro basin. It may reach a height of ninety feet but usually is a medium-sized tree. A yielder of rubber only slightly inferior to that of *Hevea brasiliensis*, *H. Benthamiana* is often tapped commercially, but it has never been used for plantation stock. Its latex is pure white. *Hevea Benthamiana* is easily recognised by the golden-brown indument on the under surface of its leaves. There appears to be comparatively little variability in this species in the undisturbed forest.

2. **Hevea brasiliensis** (Willd. ex Adr. de Juss.) Mueller-Argoviensis in Linnaea 34: 204. 1865.

With the exception of one small area west of Manáos, *Hevea brasiliensis* is apparently confined to areas in the Amazon Valley south of the Amazon River and to the Matto Grosso and Paraná (14). In most parts of the Amazon Valley, it is usually associated with periodically-flooded areas, but in the Matto Grosso of Brazil, in Bolivia and in the Madre de Dios in Peru, it abounds on high, well-drained upland areas, where it becomes a much taller and more corpulent tree, attaining a height often of 130 feet. As the outstanding species from a commercial point of view, *Hevea brasiliensis* has received by far the greatest amount of botanical study in the field. Because of our fuller knowledge of this concept, some workers have thought *Hevea brasiliensis* to be the most variable of the species; in reality, it is no more variable — and probably less so — than most of the other species. Its latex varies from a pure white to cream-white.

3. **Hevea guianensis** Aublet Hist. Pl. Guian. Fr. 2: 871. 1775.

The most widespread of the species, *Hevea guianensis* is found throughout the range of the genus and shows much morphological variability. Its

great range and its variability may possibly indicate that *Hevea guianensis* is one of the oldest species of the genus. Even though its cream-yellow latex yields a rubber of inferior quality, the species, like its variety *lutea*, is assiduously tapped over a wide area, especially in eastern Colombia. At home on well-drained upland or on high river-banks which are subject to light flooding for only a short period, *Hevea guianensis* usually becomes a gigantic tree more than one hundred feet tall, often overtopping the jungle canopy. This species and its variety *lutea* may be distinguished at once by their conspicuously erect leaflets.

3a. **Hevea guianensis** Aublet var. **lutea** (Spruce ex Benth.) Ducke et R. E. Schultes in Caldasia 3: 249. 1945.

Almost as widely distributed as *Hevea guianensis* itself, this variety can sometimes be distinguished from *Hevea guianensis* by its very conspicuously obovate and abruptly apiculate leaflets, but both vegetative and floral characters separating the two often intergrade. The latex of *Hevea guianensis* var. *lutea* usually is more deeply yellow than is that of *H. guianensis*.

4. **Hevea microphylla** Ule in Engler Bot. Jahrb. **35**: 669, *t. 1, figs. j, k, l, m.* 1905.

Without doubt the most distinct species of *Hevea*, *H. microphylla* appears to be a strict endemic of the uppermost Rio Negro basin in Brazil, Colombia and Venezuela (35). It demands low land which, flooded often to a depth of ten feet for four months during the rainy season, retains a boggy condition throughout the year. The tree has a conspicuous and characteristic swelling at the base and tapers rapidly to a slender, flexuous trunk, often reaching a height of sixty feet and supporting a very sparse crown. The pistillate flowers have an unusually well-developed torus. The capsules, with leathery instead of woody valves, are pyramidal and pointed. The fruit does not dehisce suddenly, shooting the seeds appreciable distances as in all other known species; on the contrary, it opens slowly and drops the seeds directly beneath the tree. The white latex is very watery and almost completely lacks rubber, for which reason it is never gathered by tappers. Until recently, this concept has been called *Hevea minor* Hemsley, a synonym of *H. pauciflora* var. *coriacea*.

5. **Hevea nitida** Martius ex Mueller-Argoviensis in Martius Fl. Bras. 11(2): 301. 1874.

Formerly known as *Hevea viridis* Huber, this species is one of the most interesting members of the genus. Usually a medium-sized tree with a sparse crown, growing in light caatinga-forest on sandy soil, *Hevea nitida* sometimes becomes, in areas of light inundation, a stout tree up to ninety feet in height. One of its distinguishing characters is the very shiny upper surface of the reclinate leaflets. Its thin, white latex is of no value as a source of rubber; indeed, if its latex be mixed (as has often happened when new jungle areas were opened to tapping) with that of *Hevea Benthamiana* or

H. guianensis, it acts as an anti-coagulant (24, 28). The rather disrupted distribution of *Hevea nitida* includes almost the whole Amazon Valley and the uppermost Orinoco, but the species seems to be most abundantly developed in the Rio Negro basin of Brazil and in Amazonian Colombia.

5a. **Hevea nitida** Martius ex Mueller-Argoviensis var. **toxicodendroides** (R. E. Schult. et Vinton) R. E. Schultes in Bot. Mus. Leafl. Harvard Univ. **13**: 11. 1947.

A bushy treelet, usually not much exceeding eight feet in height, *Hevea nitida* var. *toxicodendroides* is known only from the isolated, remnant, quartzitic mountains of Cretaceous age in eastern Colombia (24, 26, 28). Here, occurring on sandstone which is almost devoid of soil, the treelet grows under severe conditions of psammophytic and chersophytic drought. Nevertheless, specimens which have been planted in rich alluvial soil at Urabá, Colombia, under excessive rainfall, retain their bushy habit of growth. Unlike that of *Hevea nitida*, the latex of this variety has a relatively high percentage of caoutchouc.

6. **Hevea pauciflora** (Spruce ex Benth.) Mueller-Argoviensis in Linnaea **34**: 203. 1865.

Hevea pauciflora, known from the Rio Negro and upper Orinoco basins and from the Guianas, is not nearly so widespread nor abundant as is its variety *coriacea*. It is a rather corpulent tree with large, membranaceous (except in age) leaflets and very large seeds. The latex is white and has a low caoutchouc and high resin content.

6a. **Hevea pauciflora** (Spruce ex Benth.) Mueller-Argoviensis var. **coriacea** Ducke in Arch. Inst. Biol. Veg. Rio 239. Jan. 2, 1935.

Like *Hevea nitida*, with which it sometimes grows, this variety has a rather wide but disrupted range (15, 37). It is a small to medium-sized tree, seldom surpassing sixty feet in height, growing on rocky hillsides or high river-banks which are well drained and safe from the annual flood. The latex of *Hevea pauciflora* var. *coriacea* varies from whitish to a tawny yellow; it is never a pure white, as in the species. The leaflets, which are usually smaller than in the species, have a leathery texture from a few weeks after their appearance and become very thick-coriaceous, often somewhat marginate, in age. The seeds are very small to medium-sized.

7. **Hevea rigidifolia** (Spruce ex Benth.) Mueller-Argoviensis in Linnaea **34**: 203. 1865.

A strict endemic confined apparently to the uppermost Rio Negro basin of Brazil, Colombia and Venezuela, *Hevea rigidifolia*, like *H. pauciflora* var. *coriacea*, with which it often grows, prefers high, well-drained, sandy or friable soil supporting a light caatinga-forest. It is commonly a medium-sized tree, sixty feet in height, with a sparse crown. The latex, which usually has a slightly cream-yellow hue, is poor in rubber and high in resin.

An outstanding characteristic of *Hevea rigidifolia* lies in the extremely thick-coriaceous and very strongly revolute-marginate leaflets which are always borne in a conspicuously reclinate position.

8. **Hevea Spruceana** (Benth.) Mueller-Argoviensis in Linnaea **34**: 204. 1865.

Hevea Spruceana occurs in great abundance on low and very deeply flooded river-banks along the Amazon River itself from its mouth up to about its confluence with the Içа or Putumayo and along the lower courses of the tributaries of the lower Amazon. The trunk is conspicuously bellied at the base, and the tree has leaflets which are usually more or less densely velutinous on the under surface. The flowers seem almost never to be yellow, usually varying between a purplish brown and brown colour, and are sometimes objectionably pungent-aromatic. As its watery, white latex is almost devoid of rubber, *Hevea Spruceana* has no commercial interest to the tappers. The capsule and seeds are the largest of the genus.

MICRANDRA Bentham

Micrandra (including those species formerly accommodated in *Cunuria*) comprises some 13 species, all confined to South America (36). The genus is probably rather closely allied to *Hevea*, but it has a much wider range. Known from the entire Amazon basin and from southeastern Brazil, the Orinoco drainage-area and all of southern Venezuela, the Guianas, as well as from the Magdalena Valley in Colombia, *Micrandra* would appear to be an old genus. Only one species — *Micrandra minor* — has been of any commercial importance as a rubber producer. As in *Hevea*, the species of *Micrandra* exhibit a predilection for a wide range of ecological sites, from river-banks to mountain-slopes and from areas of heavy to light rainfall, but none is known to prefer the permanently boggy sites chosen by some of the species of *Hevea*.

In Brazil and Colombia, certain species of *Micrandra* are known as *arara-siringa* or *cunurí*.

1. **Micrandra australis** (R. E. Schult. ex Baldw. et Schult.) R. E. Schultes in Bot. Mus. Leafl. Harvard Univ. **15**: 202. 1952.

Micrandra australis is a poorly understood species known from a high plateau between two tributaries of the Rio Madeira in the central part of the Amazon basin.

2. **Micrandra bracteosa** Mueller-Argoviensis in Martius Fl. Bras. **11**(2): 290. 1874.

This species is very incompletely understood. Known only from several very old collections, it seems to be confined to coastal Brazil (Bahia).

3. **Micrandra brownsbergensis** Lanjouw Euph. Surinam, 34, *tt.* 7, 8. 1931.

A medium-sized tree occurring in the lowland rain-forests of Dutch and French Guianas.

4. **Micrandra elata** (Didrichs) Mueller-Argoviensis in Linnaea 34: 142. 1865.

Micrandra elata is an apparently rare tree of medium-size known only from southeastern Brazil (Minas Geráis and São Paulo). It is the southeasternmost representative of the genus.

5. **Micrandra glabra** (R. E. Schult. ex Baldw. et Schult.) R. E. Schultes in Bot. Mus. Leafl. Harvard Univ. **15**: 203. 1952.

A seventy-five to one hundred foot tree, this species is known from British and Dutch Guianas and from Venezuela. It grows apparently in savannah forests associated with the ancient Venezuela-Guiana land-mass.

6. **Micrandra Gleasoniana** (Croiz.) R. E. Schultes in Bot. Mus. Leafl. Harvard Univ. **15**: 203, *t. 65*. 1952.

A tree up to sixty feet in height, known only from the Mazaruni drainage-area in British Guiana, where it appears to be associated with outcrops of the Venezuela-Guiana land-mass, *Micrandra Gleasoniana* is most conspicuous because of the dense yellowish, velvety indument on the under surface of the leaves.

7. **Micrandra Lopezii** R. E. Schultes in Bot. Mus. Leafl. Harvard Univ. **15**: 204, *tt. 66, 67*. 1952.

Micrandra Lopezii, a small tree of some forty-five feet in height, is a very strict endemic known only from several stations in the uppermost Rio Negro basin of Brazil and Colombia. It inhabits sandy caatingas where the forest is very light. It is apparently allied most closely to *Micrandra glabra*. The seeds are small for the genus. *Micrandra Lopezii* has an unbuttressed trunk, but there is a variant with well developed prop-roots: *M. Lopezii* var. *anteridifera* R. E. Schult.

8. **Micrandra minor** Bentham in Hooker Bot. Journ. 6: 372. 1854.

Widespread and abundant in the Amazon Valley and the upper Orinoco basin, *Micrandra minor* is a gigantic tree, often attaining a height of one hundred and ten feet. The crown is very heavy, and the corpulent trunk is unbuttressed. This species prefers high river-banks which are inundated only at the height of the annual flood, and is never found in low-lying swampy areas. The very abundant, thick, pure white latex yields a rubber of high quality and has been tapped in the past for "Caurá rubber"; but, as the tree cannot be subjected to repeated and frequent tapping, it is not promising for planting. *Micrandra minor* superficially resembles *M. siphonioides*, and the two concepts have sometimes been thought to be identical. *Micrandra minor* never has buttresses, whereas *M. siphonioides* always has enormous tabular roots. The former species is a riparious tree,

whereas the latter always grows on sandy, well-drained upland soil. In the nerve axils, on the under side of the leaf of *Micrandra siphonioides*, there are dense tufts of yellowish hair, but the leaf of *M. minor* is wholly glabrous. The natives distinguish between the two, calling *Micrandra minor* by the Brazilian name *arara-siringa* and referring to *M. siphonioides* as *arara-siringa da caatinga*.

9. **Micrandra Rossiana** R. E. Schultes in Bot. Mus. Leafl. Harvard Univ. **15**: 211, *tt. 68, 69*. 1952.

Micrandra Rossiana has a widespread, though very disrupted, range in the northwestern part of the Amazon Valley in Brazil, Colombia and Venezuela, occurring always on high knolls far above the annual flood. It is especially abundant in the Vaupés of Colombia. With no appreciable flow of latex, this species is an unbuttressed tree up to about seventy feet in height. The prominently carunculate seeds are relatively large.

10. **Micrandra santanderiensis** Croizat in Journ. Arnold Arb. **24**: 169. 1943.

Obviously allied to *Micrandra brownsbergensis* and *M. elata*, this species is remarkable because of its distribution. The only species known west of the Andes, it occurs in the Magdalena drainage-area of Colombia.

11. **Micrandra siphonioides** Bentham in Hooker Kew Journ. **6**: 371. 1854.

This heavily buttressed caatinga-tree is abundant, albeit disruptedly distributed, in the northwestern part of the Amazon Valley from Manaos westward, being especially abundant in the Rio Negro basin of Brazil and Colombia. It is a poor yielder of latex and is never tapped. Its closest ally is *Micrandra minor*, with which it has often been confused. The crown is extraordinarily extensive, and it usually fruits in profusion, shedding great quantities of a medium-sized seed.

12. **Micrandra Spruceana** (Baill.) R. E. Schultes in Bot. Mus. Leafl. Harvard Univ. **15**: 217. 1952.

Better known under the binomial *Cunuria Spruceana* Baillon, this species is widespread on high, well drained soil in the western half of the Amazon Valley and the uppermost Orinoco. It occurs in Brazil, Colombia, Peru and Venezuela. In the Rio Negro basin of Brazil and in much of Amazonian Colombia, it is excessively abundant. It is a corpulent, well buttressed tree sometimes reaching ninety or one hundred feet in height. The capsules are borne in great abundance and yield large, glossy, reddish brown seeds very rich in oil. The white latex is very sparse and resinous and is never gathered.

13. **Micrandra Sprucei** (Muell.-Arg.) R. E. Schultes in Bot. Mus. Leafl. Harvard Univ. **15**: 218, *tt. 70, 71* (upper fig.), *72, 73*. 1952.

One of the most abundant of the caatinga-trees of the northwestern Amazon, especially in the upper Rio Negro basin of Brazil, Colombia and Venezuela, *Micrandra Sprucei* was, for a century, known only from Spruce's type collection. It is better known as *Cunuria crassipes* Mueller-Argoviensis.

VAUPESIA R. E. Schultes

A monotypic genus which seems to stand phylogenetically between *Micrandra* and *Joannesia*, *Vaupesia* is unknown except in a very restricted part of the northwest Amazon, in the basins of the Apaporis and Vaupés Rivers of Colombia and Brazil (39). The one species inhabits rocky and sterile but well-watered sites usually alongside cataracts and rapids in the rivers, where there are either quartzitic or granitic outcrops.

1. **Vaupesia cataractarum** R. E. Schultes in Bot. Mus. Leafl. Harvard Univ. 17: *27, t. 12, 14.* 1955.

Vaupesia cataractarum grows in isolated pockets, but, where it occurs, it is found in great abundance. A corpulent tree attaining a height of eighty feet, this species is, in its foliage and fruits, so similar to *Micrandra Spruceana* that the Tukano Indians of the Vaupés River employ the same name for both. The tree fruits profusely, each capsule containing three large, dull brown seeds. It is of no value as a latex-tree.

III.

Reports concerning the use of rubber seeds as food constituted merely curious ethnobotanical information until very recently. About a decade ago, these reports were taken up and, through a series of successively more far-reaching postulations, comestible use by primitive peoples of rubber seeds was credited with having had directly or indirectly really titanic influences upon the evolution of *Hevea*. So firmly entrenched have these postulations become in the literature in this short time that it behooves us to study them with an eye alert to their soundness. It will serve our purposes best, if the postulations be here quoted in the words of their proponents and as they were presented, from their prudent beginnings to their present strident positiveness.

In 1947, Baldwin (4) and Seibert (40) mentioned the fact that the Indians of the northwest Amazon eat *Hevea* seeds, and they utilised it as one argument in a series which they advanced to explain certain presumed steps in the evolutionary history of the genus.

Baldwin (4) assumed that, when forest is felled for house sites, the natives spare *Hevea* trees either because the trees are a source of latex "or, in some areas, because the seed are eaten, or because the wood is poor fuel." He pointed out that such a practice would present "excellent opportunities for hybrid swarms to become established." To the best of my knowledge, this is the first time that the primitive and probably earliest use

of *Hevea* has been considered thoughtfully from the point of view of what effect it might have had on the evolution of the genus.

Keenly interested in the phyletic significance of certain differences which he had observed in the loss of oil from seeds of a number of species of *Hevea*, Baldwin (7) has implied a correlation between oil content of the seed and their use as a food.

> That seed of both *H. rigidifolia* and *H. Kunthiana* [usually known as *H. pauciflora*] lose oil in significant amounts suggests close genetic relationships between these species. Baldwin . . . stated that their seed are much alike and that the natives of the upper Rio Negro eat the seed of both species: he found a tree of *H. rigidifolia* that had been cut for its almost-mature seed and recorded that trees of *H. Kunthiana* are not uncommonly planted for their edible seed. Though the natives 'designate the latter tree *seringa*, they say it has seed like *cunury*.' Baldwin and Schultes . . . discussed the use of seed of *cunury* — i.e., of *Cunuria*, a genus with affinities to *Hevea* — as food of Amazonian Indians . . . And Baldwin . . . has mentioned the possibility of introgression between these genera. Pertinent here is the fact that *Cunuria* seed among my collections evidence no loss of oil. . . .
>
> That the Amazonian native seems especially to select for food the seed of *H. rigidifolia* and of *H. Kunthiana* and that oil escapes freely from seed of these species are reasons for according this phase of the genus particular study.

Seibert (41) took this thesis further, arguing as follows:

> Through its value as a food plant to the Indians of the Rio Negro region, it appears that *Hevea* became a semi-domesticated tree. Its domestication along the major waterways, in clearings, edges of villages and camp-sites followed a pattern of conscious or unconscious selection for seed production. The planting of certain species in the vicinity of other wild species substantially aided the process of interspecific hybridization. Once established in clearings, the mature hybrids and introgressive hybrids are (at least in part) capable of competing with the encroaching second growth. Several centuries of this slow process seem to have played a conspicuous part in the resultant hodge-podge of variables turning up as representative collections of *Hevea* from the Rio Negro. . . .[3] From present evidence, it appears that *Hevea pauciflora* has been the species of *Hevea* most cultivated by the Indians of the Rio Negro and upper Amazon.

Under *Hevea pauciflora* (in which he included *H. pauciflora* var. *coriacea*), Seibert (40) went farther by saying that "in the hundreds of years Indians have been along the Rio Negro they have . . . distributed the species outside of its natural habitat." He entertains the possibility that *Hevea pauciflora* got as far as Iquitos, Perú, through the agency of man. "It would not be too hard," he argued (40) "to presume that *Hevea pauciflora* may have been introduced into Iquitos before the white man arrived."

[3] There is a much greater development of speciation in *Hevea* in the northwest Amazon, but, on the basis of the available collections and on several years of field work along the Rio Negro and its western affluents, I venture to say that there is no greater variation here than in most other parts of the Amazon which are as well known. Certainly, so far as *Hevea* is concerned, there is no "hodge-podge of variables" in the area.

Seibert presented his postulations prudently, usually avoiding categorical statements. He undoubtedly hoped to stir up discussion and evaluation of his hypothesis. Unfortunately, there has developed a tendency recently to accept Seibert's suggestions *in toto* and to present them as well established and proven facts, with no inkling that they are highly hypothetical from beginning to end.

Anderson (1), for example, saw the problem as follows:

> Apparently the species was first cultivated for its edible nuts . . . Either accidentally or with intent, seedlings from wild trees came up in clearings where they were being used for food. These areas were often outside the natural range of that species or variety and sometimes within pollination distance of other species. Consequently, these isolated trees tended to be cross-pollinated. Under the primitive agriculture of these areas, clearings were occupied for a time and then deserted. As the disturbed land gradually reverted to jungle, there were many opportunities for the hybrid seedlings of the isolated nut trees to germinate and survive. They crossed back to the native species of that vicinity, and thus the process of introgression might have started in hundreds of little clearings in the jungle. The more or less casual use of *Hevea* for its edible nuts increased the natural introgression between some of the species. When man gradually learned that the latex of *Hevea* also had its applications, he already had at hand variable, introgressed, semi-domesticated populations, in which trees superior in latex were more likely to be found.

More recently, Anderson (2) has taken the same theme to much bolder lengths, weaving into the story as previously elaborated additional and highly imaginative aspects. He states in part:

> There is a great variation in the rubber content of the supposedly wild trees; some of the higher-yielding strains trace back to sites which are now part of the jungle but which indicate clearly that they had been village clearings before they were engulfed by the rapidly regenerating tropical brush . . . primitive man first domesticated the Pará rubber tree for its nuts . . . By doing this, they brought into their small and transient villages trees which were not just a random selection of the original wild species but just those with superior nuts, or a superior yield of nuts. In doing so, they frequently brought in trees which were not native to that immediate area . . . As these clearings were deserted, the alien trees crossed with those in the immediate vicinity and thus in more than one clearing there eventually developed mongrel swarms of Pará rubber trees, which had the heightened variability characteristic of mongrels. It was among them that some of our most potentially valuable breeding material was located when we eventually became much more interested in the milky sap than in the nuts.

In considering the "purity" of the *Hevea brasiliensis* material which was first imported into the Far East from Brazil, Dijkman (10) has cited some of Seibert's postulations in connexion with the use of *Hevea* seed as a food and has accepted as fact Seibert's thesis that the Indians spread *Hevea pauciflora* far and wide.

Seibert, in addition, has collected evidence of penetration of *H. pauciflora* into the *H. brasiliensis* complex referred to above. He assumes this probably first

began as a result of the natural enlargement of the original habitat; but the process seems to have been considerably hastened by the autochthonous inhabitants of the continent. The seed of this species and/or its expressions are eaten by the Indians, who carried the seed with them on their migrations and brought *H. pauciflora* under cultivation in their new settlements. . . . This man-caused spreading has created the impetus for its adaptation to a wide range of extreme climatic conditions.

Even a hasty review of the several passages which I have quoted above shows that an extraordinary amount of theoretical importance is being given to reports on the use of *Hevea* seeds as a food and far-reaching assumptions are being made in an attempt to build up a plausible sequence of events to fit into the hypotheses propounded. A moment's hesitation and thought will recommend caution and forfend unbridled play.

What, then, are the ethnobotanical facts, and how do these facts, bereft of unfounded trimmings, fit into the hypotheses which we have just reviewed?

IV.

Oddly enough, historical references give us very little information on the use of *Hevea*, *Micrandra* or *Vaupesia* seeds as a comestible. There may be several explanations for this. One reason which we must bear in mind is the paucity of reliable ethnobotanical records for the vast Amazonian forest area. Another may be the ease with which travellers could have overlooked this strange food, for the seeds of these jungle trees are normally available for but a very short time (about one month) each year and, as they do not keep, they must be used at once. It is hard to account for the dearth of references to this custom, even in the several detailed anthropological accounts of the Indians of the northwest Amazon written by men who had spent many months, even years, in the region. This silence in anthropological writings is all the less understandable when one realises that sometimes tribal festivals or dances are centered around the harvest of *seringa* or *cunurí* seeds for food.

To Fusée Aublet must go the credit of first reporting the use of rubber seeds as a food. In his description of *Hevea guianensis*, in 1775, he (3) wrote of certain Indians of French Guiana:

> The Galibis [Caribs] and Garipons carefully gather the nuts from the fruits of this tree. They keep them and eat them with enjoyment. I have witnessed their assiduity in collecting the seeds when they come upon these trees on trips that I have made with them; I have imitated them. I have eaten many of these nuts without feeling any disturbance whatsoever.

This passage merits attention not only as the earliest report of this use of rubber seeds but also as the only report which apparently ignores their cyanic content. It is not easy to interpret Aublet's statement that the Indians "keep" the seeds, for they spoil with great rapidity. Furthermore, the seeds of *Hevea* and its allies *Micrandra* and *Vaupesia* are known to be

highly toxic to man, until the cyanic poisons are removed by long soaking or by boiling.

The next reference to the eating of *Hevea* seeds is that of the botanist Richard Spruce who spent seven years in the Amazon Valley and who, through his collecting, greatly advanced our knowledge of *Hevea* and its relatives. In 1854, Bentham (9) published Spruce's manuscript notes on *Hevea*, and we find the following report:

> The seeds are an excellent bait for fish. Macaws eat them greedily, but to man and quadrupeds they are poisonous in a fresh state. The Indians on the Uaupés render them eatable in this way: after being boiled twenty-four hours, the liquor is strained off, and the mass that remains has something the colour and consistence of rice long boiled. Eaten along with fish it is exceedingly savoury.

It is of the utmost import here to make note that Spruce did not designate any *one* species of *Hevea* as a source of edible seeds. His discussion referred to the genus as a whole. There can be little doubt that Spruce meant that the Indians of the Vaupés River used any or all of the species as a source of comestible "nuts."

During my more than a decade of field work on *Hevea* and its relatives in the Amazon Valley, I have given critical attention to the part which these plants play in the economy and lore of the Indians, especially of the more primitive tribes which do not engage in rubber-tapping work.

The first observation which I must make is that, as far as the literature and my own observations attest, the seeds of *Hevea* and *Micrandra* are used regularly as an annual food exclusively in the northwestern part of the Amazon Valley — that is, in the basin of the Rio Negro in Brazil and in the Comisarías del Vaupés and Amazonas in Colombia. I have never heard reports amongst the inhabitants of other parts of the Amazon Valley, and botanists who have worked elsewhere tell me that they have not heard of the custom. Seibert, who spent a number of years in eastern Peru and who became extremely interested in Spruce's report of the food-use of rubber seeds, does not record it from any part of Peru. Dr. Adolpho Ducke, who has collected plants in all parts of the Amazon Valley for half a century, agrees that this aboriginal custom is peculiar to the northwest. One must needs, of course, distinguish between the regular and often ceremonial consumption of the seeds, on the one hand, and the occasional eating of them in isolated instances as a last resort during great famine, on the other hand.

The fundamental importance of this fact is at once evident. Restricted culture-trait that it is, the habit of eating rubber seeds could not have had the widespread effect postulated by Anderson and Dijkman. Baldwin realised that this use of the seeds was localised, but Seibert stated that it was a custom "within the Amazon Valley itself" and suggested man as an instrument of spread over great distances. Dijkman had the Indians carrying the seeds of *Hevea pauciflora* "with them on their migrations and brought *H. pauciflora* under cultivation in their new settlements," and he

speaks of "this man-caused spreading" as having helped adapt the species to a "wide range of extreme climatic conditions." Even were the custom of eating the seeds widespread, it would be impossible for Indians migrating any distance in open dugout canoes to carry along the notoriously short-lived rubber seeds in a viable state.

There is a second important observation which I must make. It is very probable that the seeds of all of the species of *Hevea* occurring in the northwest Amazon are eaten.

There would seem to have been a tendency to lay more stress on the importance of *Hevea pauciflora* as a source of food than on any other species. This must be examined critically, for there would seem likewise to be an implication that this species, partly because of its "cultivation" and "domestication" through man's interest in it as a source of food, has led to a great degree of intraspecific variation and has similarly caused this species to "penetrate" others and so influence markedly the course of development of the genus. Baldwin (4, 5, 7) reported that the natives of the upper Rio Negro select the seeds especially of *Hevea pauciflora* and *H. rigidifolia* for food; and Seibert (41) felt that the available evidence pointed to *H. pauciflora* as the species preferred.

There is no basis for the supposition that one or two species are preferred over others. In the northwest Amazon, all known species of *Hevea* but two — *H. brasiliensis* and *H. Spruceana* — are represented. Of the six species occurring in the region, the seeds of five of them are used as food. Whilst living in Indian sites in eastern Colombia, I have eaten the seeds from several species myself. Ducke (12) reported that the natives living along the Curicuriarí eat the seeds of more than one species of *Hevea*.

Hevea microphylla seeds, which are unusually large for the genus, do not seem to be gathered for food; and I think the reason for this is only the difficulty of harvesting them. *Hevea microphylla*, as we have seen above, grows in almost permanent bogs, and the *sarapó* and other fish, spawning in this season in the wake of the flooded forests, snap the seeds up with great alacrity. The capsules do not open with explosive violence, so the seeds are not shed in quantity, as in other species; when the capsule opens gently, the seeds fall one by one into the water below. The tiny seeds of *Hevea nitida* var. *toxicodendroides* are, apparently, never gathered for food because of their size.

If there be any rubber trees the seeds of which are more commonly used as food in the northwest Amazon, it is neither *Hevea pauciflora* nor *H. rigidifolia* but *Hevea guianensis* and *H. guianensis* var. *lutea*. This is due not to any preference but to the greater abundance and availability of these trees. I have seen collecting parties gathering the seeds of *Hevea guianensis* and its var. *lutea* amongst the Makunas of the lower Apaporis River, the Taiwanos of the Kananarí and the Kubeos of the Vaupés in Colombia. I have eaten mash from the seeds of *Hevea guianensis* in the country of the Kuripakos at the headwaters of the Guainía in Colombia. The Yukunas and Tanimukas of the Miritiparaná in Colombia make unleavened cakes from the seeds of *Hevea guianensis* var. *lutea* and of *Micrandra Spruceana*

as the principal starch food in their beautiful annual Dance of the Cunurí or Wĕ-ra. In this case, there seems to be a preference for seeds of *Hevea guianensis* var. *lutea* over those of *H. nitida*, even though, when the seeds are used as food in everyday life without any connexion with this semi-religious dance, both are used indiscriminately. There is probably some ceremonial reason for the choice, for the preference is a strict trait. The only "explanation" which I could get was that *Hevea guianensis* var. *lutea* is "cousin to" *Micrandra Spruceana*. Both tribes have distinctive names for these two rubbers: the Yukunas refer to *Hevea guianensis* var. *lutea* as *hĕ-che* (a name interestingly similar to that of *Micrandra Spruceana*: *yĕ-cha*) and to *H. nitida* as *ya-wá-ro*; the Tanimukas refer to the former as *wãn-hoó-a*, to the latter as *wãn-hoó-a-ma-ka-na*. The Miritiparaná is the only region in which I have found the mash or pulp from the seeds of either *Hevea* or *Micrandra* elaborated into cakes.

Hevea nitida is very widely employed in the northwest Amazon as the source of edible seeds. This tree, as we have seen, grows either in jungle which is but slightly flooded at seed-time or in upland forest on well-drained sand. Needless to say, it is usually the latter instead of the former habitat to which the Indians, in search of rubber seeds, repair. The reasons are clear. It is much more difficult to walk through a flooded forest, and the seeds are much less abundant because of the great quantities eaten by spawning fish. I have seen seeds of *Hevea nitida* gathered for food or eaten in Colombia by the Taiwanos and Kabuyarís of the Kananarí, the Tukanos, Desanos, Kubeos and Gwananos of the Vaupés, the Yukunas and Tanimukas of the Miritiparaná and, in Brazil, by the Tukanos of the Uaupés and Negro. Along the banks of the Vaupés River above Mitú, *Hevea guianensis* var. *lutea* and *H. nitida* often grow intermixed in the forests and, in this case, the Kubeos gather both indiscriminately, showing no preference for one over the other. This is likewise true amongst the Tukanos of the Tikié in Brazil.

I have not seen *Hevea Benthamiana* seed used, but the Kuripako Indians along the lower Guainía and a few Mirañas on the Caquetá in Colombia have informed me that this species may be used as a food, and Baldwin (5) reports its use on the Uaupés River of Brazil. It is easily understood why, in a region with highland species as well, *Hevea Benthamiana* would be neglected as a source of seeds: at harvest time, the rivers are at their highest, and *Hevea Benthamiana* stands in from three to ten feet of water.

There remain to discuss only *Hevea rigidifolia* and *H. pauciflora*, the two species which Baldwin suggested were the most important as a source of food-seed. *Hevea rigidifolia* is a comparatively localised species, but, as it grows in abundance in pockets of light forest on well-drained sandy soil, it is visited by the natives who live in its vicinity. It is eaten in quantity by the Tukanos and Desanos of that part of the Vaupés and Papurí Rivers which form the boundary between Brazil and Colombia. *Hevea pauciflora* seeds seem to be eaten mainly by the natives along the upper course of the Negro and the seeds of *H. pauciflora* var. *coriacea*,

not well liked because of their smaller size, are used in several areas along the Vaupés, Guainía and Apaporis Rivers in Colombia.

As pointed out above, the Indians along the main course of the Amazon River are not known to eat rubber seeds, unless conditions of famine prevail. It will be of interest here to record that I saw a group of Tikunas near Leticia, Colombia, prepare seeds of *Hevea brasiliensis* and eat the mash with baked fish. These Indians, who were engaged in collecting, under my direction, several tons of rubber seeds (27), had eaten all their fariña meal and were forced to turn to rubber seeds. They made it clear that these were only an emergency food. I mention this merely because I have not been able to find any reference on the edibility of the seeds of *Hevea brasiliensis*.

From the foregoing information, it ought to be clear that the seeds of most, if not all, species of *Hevea* can and are taken as food in the northwest Amazon.

It might be worthwhile here to look at the situation in *Micrandra* and *Vaupesia*.

Again we turn to Spruce for our earliest knowledge of *Micrandra* seed as a food. On labels of specimens of *cunuri* (*Micrandra Spruceana*) collected in the uppermost Rio Negro basin in 1853 and preserved at Kew, Spruce made the following annotation (8):

> On the Uaupés and around São Gabriel [Estado do Amazonas, Rio Negro, Brazil], a large tree obviously allied to *Siphonia* [*Hevea*], called by the Indians *Cunurí*, is frequent in the forest. It has large arched buttresses at the base, like the *uacu* [*Monopteryx Uaucu* Spruce ex Benth.], from which it is distinguished by milk flowing from it when wounded. I have not yet seen its flowers or fruits, but the Indians describe the latter as tricoccous, quite as in Siphonia, and they use the seeds in a similar manner. These being boiled 24 hours yield a small quantity of oil, which serves for lamps. The pulpy mass into which the seeds have now fallen is packed in a basket and kept under water 3 days to sweeten; when taken out, it has a pleasant taste and no ill smell. It is eaten without the addition of anything else and may be kept a long time, but if the seeds have not been well boiled, it is a quick poison, and Indians have fallen victims to its incautious use.

In 1854, Spruce (19) reported that from the seeds of "*cunurí*, abundant on the alto Rio Negro, Orinoco, Casiquiare, Pacimoni, etc., the Indians prepare a paste resembling cream-cheese in appearance and taste. The seeds are first boiled and then steeped for some days under water, after which they are broken up by the hand. In the boiling, a quantity of oil is said to be collected . . . it is said to be as bitter as andiroba oil, but to afford an excellent light."

Apparently nothing more was written on *cunurí* seeds as food until recent years. Referring to *Micrandra Spruceana*, Ducke reported it for the Indians of the upper Rio Negro in 1934 (20). In 1943, Paul H. Allen (herbarium specimen *Allen 3063*) recorded a comparable use of *cunuri* by the Tukanoan Indians living on the Rio Papuri, an affluent of the

Vaupes and part of the boundary between Brazil and Colombia. In 1944, Baldwin found the seeds of *cunuri* eaten in the upper Rio Negro-Rio Uaupes region of Brazil (Baldwin et Schultes loc. cit. 344). And, in 1945, I (25) called attention to the use of *cunuri* seeds as food on the lower Caqueta and its affluents in Colombia:

> The seeds of *Cunuria Spruceana* apparently contain a cyanide and, according to the natives, are extremely poisonous when taken internally in the crude state. The Indians of the lower Caquetá, however, consume quantities of the seeds in the form of a greyish mash which is prepared by boiling the pulp in three waters to remove the poison. This mash has a peculiar taste, somewhat like burnt potato. According to the natives, salt must not be added to this mash.

This was the first of many observations pointing to the value of *Micrandra Spruceana* as a food. Since then, I have witnessed the preparation of this food and have, on a number of occasions, partaken of it myself. *Micrandra* and *Hevea* fruit simultaneously. The seed of *Micrandra Spruceana* is much more highly esteemed than that of any other species of *Micrandra* and more than that of any *Hevea*, wherefore, if *Micrandra Spruceana* occurs in abundance in a given region, very little *Hevea* seed is gathered. *Micrandra Spruceana* grows on light sandy soil which never floods, the tree fruits prodigiously and the seeds are large and full of a firm pulp which handles easily in boiling. In former years, the oil which came to the surface during boiling was used in lamps, so that these seeds were rather valuable in the native economy.

According to reports which I have gleaned in the field, *cunurí* seeds are eaten by the Barasanas, Desanos, Gwananos, Kabuyaris, Karihonas, Kubeos, Kuripakos, Makunas, Miranas, Taiwanos, Tanimukas, Tatuyos, Tukanos and Yukunas in eastern Colombia. They are likewise used by some of the natives in the upper Rio Negro basin of Brazil and possibly also in the very uppermost Orinoco. I have witnessed the preparation and use of these seeds by the Karihonas, Yukunas and Tukanos. In all cases are the preparations similar: several boilings are always employed to remove the cyanic poisons.

Without a doubt, one of the most interesting ways of using *cunurí* seeds is the making of unleavened "bread" or casabe for the *Wĕ-ra* or Dance of the Cunuri of the Yukuna and Tanimuka Indians. A most beautiful dance, the Wĕ-ra, with the whole tribe participating, lasts for forty-eight hours, This dance takes place during the seeding-time of the *cunurí*, which is normally in March. Great groups of young men make ceremonial trips to areas of the forest where *Micrandra Spruceana* grows in abundance, large baskets are woven on the spot, and these are filled with seeds. Carried back to the house where the dance is to be held, the seeds are given over to the women who immediately start the process of boiling and washing out the poisons. The process is very similar to that used to prepare the meal or fariña from poison *Manihot*, and, indeed, it is the same or a similar poison which must be removed. After several boilings and washings, the damp mash is gently toasted on a flat plate over the fire and is reduced to a fine

greyish white meal. This is then made into *casabe* or unleavened bread, in much the same way as fariña (from *Manihot*) is used to make *casabe* cakes. Often the *cunuri* flour is, as pointed out above, mixed with flour from the seeds of *Hevea guianensis* var. *lutea*, but usually *Micrandra Spruceana* is used alone. The casabe cakes thus prepared are, together with smoked boar- or tapir-meat, the chief food of the dance.

The seeds of at least two other species of *Micrandra* are eaten in the northwest Amazon, but they seem to be used much less frequently than *M. Spruceana*. Along the Papuri River, in Colombia and Brazil, the Tukanos sometimes gather the seed of *Micrandra Sprucei* which are strewn abundantly on the floor of the sandy caatinga forest where this species is so common. *Micrandra Sprucei* perhaps has more oil in its seeds than has *M. Spruceana*. Its Tukano name *wa-só-nĕ-nĕ* means "light-rubber" ("wa-so" = *Hevea* and "nĕ-nĕ = light), probably in reference to the use of the oil boiled from the seeds to light lamps. On the Piraparaná River, the seeds of *Micrandra Rossiana* are used as food. In all of these species, the process of boiling the seeds several times to remove the poisons and oils is identical.

It will be of interest to point out that the seeds of *Micrandra glabra* have been reported (8) as "edible" in British Guiana.

Large and fleshy, the seeds of *Vaupesia cataractarum* are a favourite food of the Desano Indians along the Vaupes River between Mitu and Javarete. The extraordinarily abundant harvest each year attracts bands of Indians, and huge canoe-loads of seeds are taken back to malocas in the neighbourhood. So far as I could learn, the method of preparing these seeds is the same as for *Micrandra*. The great profusion of seeds and the ease of gathering them on the high, well-drained slopes near rapids account for the natives' predilection for *Vaupesia* over all species of *Micrandra* and *Hevea*.

What has been outlined above would seem to show rather positively that any postulations resting on the supposition that the Indians choose only one or two species of *Hevea* as a food-source are without foundation in fact.

We must next turn our thoughts towards a consideration of the claims of cultivation or "domestication" of *Hevea* as a wild nut tree. What are the facts in this regard?

Both Seibert and Baldwin base their principal postulation on the fact that along the Rio Negro, where they feel that *Hevea* shows especial variability, the Indians eat rubber seeds. Seibert further allows himself to suggest that it was a custom "within the Amazon Valley itself" for "many an Indian to transplant seedlings from jungle to dooryard." This custom I have never seen amongst Indians. Indeed, I have never seen a *Hevea* tree growing — either planted or as a survival from felling — in the garden of the house of any primitive Indian anywhere in the Amazon Valley, including the northwestern part.

Here, we must distinguish between the primitive aborigine and the civilised rubber tapper (be he pure Indian, white or half-breed), who, in felling a few square feet of virgin jungle for his temporary shack, where he lives in the dry season only whilst tapping rubber, will almost never sacri-

fice a wild *Hevea* tree. The tappers' little palm-thatch huts and their clearings often will be lorded over by two or three majestic rubber trees that have been spared, in part because they are tapped on the tapper's regular daily rounds and in part for sentimental reasons ("the goose that lays the golden egg"). There is no such custom as planting in these little jungle plots. Nor are the tappers interested in the seeds as a source of food, partly because it is only the uncivilised Indian apparently who will eat them and partly because the seeds fall at the time of high water, when the tapper and his family never use the hut, which is under water, but have moved back to a town to their permanent home.

Even were we to vouchsafe that the tappers planted seedlings or spared trees near their temporary jungle dwellings, it would be irrelevant, insofar as any appreciable effect which these isolated trees may have had on the evolutionary course of the genus. For, prior to a century ago, there was no widespread use of rubber and, consequently, no tapping industry had as yet grown up which brought thousands of workers into intimate association with wild rubber trees. Even if the isolated trees spared by the lonely tapper near his hut had had the extreme effect through hybridisation with other trees of the vicinity, which Seibert and Baldwin propose and Anderson and Dijkman accept, the effects would not yet — in only one hundred years — be seen on the large scale and over the vast area that have been suggested. Nor can such casual cultivation be termed "domestication."

That Anderson considers the effects to have been appreciable over a wide area for hundreds of years is evident when he says (1):

> When man gradually learned that the latex of *Hevea* also had its applications, he already had at hand variable, introgressed, semi-domesticated populations, in which trees superior in latex were more likely to be found. The extent and frequency of introgression must certainly vary greatly with the type of agriculture that is being practiced. Under the jungle-clearing pattern, like that just described for *Hevea*, it must have been at a maximum.

And further evidence of Anderson's lack of knowledge of Indian life in the northwest Amazon is shown by his statements that primitive man, having domesticated the rubber tree for its seeds, "brought into their small and transient villages" for planting trees selected for "superior nuts or a superior yield of nuts." This implies that the Indian selected for seeds, which, of course, with his very rudimentary agriculture, he would never have done, even had he planted the rubber trees.

Anderson refers to "supposedly wild trees" which he pictures as populating sites "now part of the jungle, but which indicate clearly that they had been village clearings before they were engulfed by the rapidly regenerating tropical brush." The truth of the matter is that the climatic climax of the northwest Amazon, as in other tropical rain-forests, is extraordinarily slow at taking over cleared areas, through numerous secondary successions. Literally centuries pass before the virgin or primary forest asserts itself, and one need not be a botanist to point out a patch where human dwelling

once disrupted the natural cover. This is so well known (23) that it need not here be discussed in any detail.

Anderson's statement that the "supposedly wild trees" of secondary communities supplied "some of our most potentially valuable breeding material" for high yield of latex is not borne out by the record of selection of élite jungle trees which botanist-explorers of the United States Department of Agriculture carried out in the Amazon Valley during the past ten or twelve years. Almost all of the most promising selections made by these botanists in Brazil, Colombia and Peru were of individuals growing in primary forest. In my own work of selection, for example, I was wont to avoid trees not in the climatic climax forest because of possible external influences on yield of latex which unnatural conditions in successive forests may have had.

It is true that, here and there along the Rio Negro and lower Uaupés in Brazil, groups of rubber trees — representing usually *Hevea guianensis* and *H. pauciflora* — grow near habitations or at abandoned house-sites under conditions that suggest that they might have been planted. I have seen such sites, and I have not the slightest doubt that they were planted. But this cultivation, it is of the most extreme interest to point out, is recent, dating no earlier than the beginnings of the rubber boom in the middle of the last century. And, in all cases, they are found at the sites inhabited by *caboclos* or half-breeds, never at settlements of uncivilised Indians. These people, though they are not of pure Indian blood and are civilised, may use *Hevea* seeds as a food, *but only when famine threatens*, not with the regularity and in the near-ceremonial way of the primitive Indian. And it must be emphasized here that the sites where one finds rubber trees under conditions suggestive of cultivation are not many. Surely, this "cultivation" would have to have been far more widespread and common to have had anywhere near the influence through hybridisation and introgressive hybridisation which Anderson and Dijkman present as established history.

If we contine our critical examination, we find that it is doubtful in the extreme that the *Hevea* trees which we see growing near houses along the Rio Negro were planted deliberately as a source of food. They may have been set out or spared in felling merely because they were "seringueiras" (rubber trees), even though neither of these two species is the one that is widely tapped for rubber along the Rio Negro. There is, nonetheless, an innate aversion to destroying any sort of rubber tree. And we must likewise consider the possibility that, as in the case of several other trees which yield no economic product, the rubber trees were set out merely as curiosities or ornamentals. Be that as it may, the unadorned facts about cultivation are these: (a) primitive Indians have not cultivated and do not now cultivate or care for rubber in any special way in their farms; (b) what little cultivation there is has been done by civilised inhabitants engaged directly or indirectly in rubber tapping; and (c) such cultivation on the Rio Negro is of relatively recent incipience and is extremely limited and localised.

A moment's thought will elucidate some of the reasons why the Indian never cultivates rubber and *cunurí* trees as a source of food.

Before the days of their reduction to civilisation, the Indians probably gathered *Hevea* and *Micrandra* seed as they do to-day: from wild trees. Many are the wild trees in the jungle that are visited every year in their fruiting time by Indians who often journey for several days to gather the nuts. I have seen this repeatedly in the Colombian Amazonia. No Indian relies upon rubber or *cunurí* trees planted or left standing in the yuca and coca fields around his house. All, without exception, garner their supply from the forest. When one lives long enough with these people, one realises the obvious and logical reason for this custom: the Indian enjoys such a harvesting trip through the jungle. It is a harvest that takes place but once a year, and it has, through the ages, come to be rather a ceremony or a kind of hunting task much to the Indian's liking. It is man's sport, whereas agriculture is left to the women. He would never think of giving up this enjoyment for the dullness of picking up the seeds near his house.

An Indian will live but a few years at one site. When he fells a patch for a house-site, the soil is leached out in a few years, and the leaf-cutting ant usually has multiplied to such an extent that it is a physical impossibility to continue to inhabit the site. Why, then, should he plant a tree that will not bear fruit in any appreciable amount under fifteen or more years, especially when the woods around his house or within easy journey are full of rubber trees? The answer is, of course, that he does not plant it at all. He might leave an occasional tree standing when he fells, but, as pointed out above, I have yet to see a rubber tree spared in the vicinity of a primitive Indian's dwelling.

Still another — and perhaps the most important — reason for not planting *Hevea* is fear of falling trees near dwelling places. None of the Indians of the northwest Amazon allows isolated trees to remain anywhere near the sites chosen for house-raising. The forest is felled clean: not one tree of any size is left standing and none is planted. Wind-storms in the Amazon are not infrequent and the sturdiest-looking trunk might easily be hollowed by rot and termite and an easy prey to the first strong blow. About the tallest tree that one sees near Indian habitations is the palm, *Guilielma speciosa*, but, as this medium-sized fruit-tree is rarely, if ever, victim of rot and, as its crown is light, it does not present the danger of falling that so often attends dicotyledonary trees of the forest.

The all-important theme in the postulations presented by Baldwin, Seibert, Anderson and Dijkman is that cultivation for edible seeds created optimum conditions for introgressive hybridisation. They give introgressive hybridisation supreme importance in *Hevea* evolution. It is not my purpose in this paper to discuss the role which this process may or may not have had, except to say that I hold that *Hevea* is probably no more variable than many other genera of tropical trees and that introgressive hybridisation has not had anywhere near the importance which is claimed for it. It is a temptation to overwork new approaches such as this, and especially so when "evidence" can be elaborated to present a

plausible series of arguments. I need not consider introgressive hybridisation here in detail simply because, as the summary and conclusion below bring out, the conditions which are stated to encourage wide-scale crossing and back-crossing to native species of *Hevea* do not exist and never did.[4]

Even though it be quite clear that extensive hybridisation of species of *Hevea* has not come to pass as a result of "domestication" of the rubber

FIGURE 2. Communal Makuna Indian house or *maloca*, Río Popeyacá, Colombia. Even though, in some tribes, the forest is close to houses, isolated forest trees are rarely, if ever, left standing near dwellings. Amongs most Indians of eastern Colombia, enormous clearings are made in the centre of which the house is built; in this case, too, all trees of any size are felled. The palm which is planted near the dwelling is *Guilielma speciosa*.

[4] Since the preparation of this paper, I have had the opportunity of reading an extremely interesting article by J. G. Bouychou of the Institut Français du Caoutchouc in Paris ("Note sur l'amelioration de l'Hevea" ms. (1955). Bouychou has postulated, as a partial basis for his proposed program of *Hevea* improvement, that the wild rubber trees in the Amazonian forest are highly inbred. This has resulted, according to Bouychou, from the wide isolation of the individual trees. The discovery that midges are the chief, if not the only, natural pollinators of *Hevea* and that *Hevea* pollen normally is not shed as far as the usual distance between individual trees in the forest are offered as support of this postulation. Without entering into a thorough examination of Bouychou's novel point of view, I may say here that many field observations which I have made in the forest as well as some of the results of recent selection and breeding work would seem to support the hypothesis which, of course, is diametrically the opposite of that proposed by Baldwin and Seibert.

tree for food, we still must grant that natural hybridisation probably has had some part in the evolution of the genus. We know that there are no barriers to hybridisation between the species, all of which have been crossed artificially.

In areas where man has caused great upheaval in the natural vegetation, we have undoubted proof of crossing. This is true of such places as the outskirts of the towns of Manáos and Iquitos (13, 37, 40). Specimens collected in such localities exhibit extremes of variation and all possible intergrades, some of which have erroneously been described, in the past, as varieties or forms. Trees left standing alone in extensively cleared areas are disrupted in their flowering rhythm and blossom almost all year through. This, together with their proximity with no interfering forest canopy, permits different species to cross freely. But even this clearing, extensive as it is in several localities, has happened only in recent times and can have had no appreciable effect on generic evolution.

Conditions are very different in the forest. Sometimes — though not so frequently as often supposed — two or more species grow together. I have noticed in the Amazon, however, that each species seems to have its own flowering time. To be sure, all species of *Hevea* flower at the beginning of the dry season, but all do not blossom in strict simultaneity. Pistillate flowers in *Hevea* are known to have a relatively short period of receptiveness (three or four days in *H. brasiliensis* (17)). There is enough disjunctiveness in flowering times to prevent appreciable natural hybridisation. That there is really little crossing in nature is borne out by long study of trees in the field and by close examination of herbarium specimens, both of which indicate that *Hevea* is not excessively variable.

This may seem to be at sharp variance with those who see every variation as evidence of "penetration" of genes from alien species. It is not, however, at variance with what I have found in the field, and Ducke (15), after more extensive field work on the genus than any living botanist, concurs. Consequently, I am forced to differ most vehemently with those who consider that in wild *Hevea* "introgression . . . is readily perceptible and of great biological import . . ." and that "one can find its influence . . . for all the species" (6).

SUMMARY

1. The Indians of the northwest Amazon utilise the seeds of a number of species of *Hevea*, *Micrandra* and *Vaupesia* regularly each year and sometimes ceremonially as a food.

2. Recent hypotheses have postulated that a) because of their interest in *Hevea* as a food-plant, the Indians cultivated trees which were selected for superior nuts or yield of nuts; b) species were carried by Indians for planting to areas far beyond their natural range; c) trees of very different provenience were planted together; d) these cultivations were later abandoned to the jungle; e) the plantings greatly enhanced the opportunities for hybridisation, and the hybrid offspring in turn crossed back to the

native, local species; f) this led to "mongrel swarms" with the excessive "variability characteristic of mongrels."

3. An exposition of the facts as found through long field work in the northwest Amazon does not support these hypotheses because a) the Indian uses seeds from wild trees and never cultivates them; b) trees occur near a few house-sites under conditions which might possibly be cultivation, but these were not planted out by the primitive Indian who eats seeds and are of such recent cultivation that they could not have had any appreciable effect on the evolution of the genus; c) due to its very short-lived seeds, *Hevea* could not be carried about by Indians over wide areas on their migrations.

CONCLUSION

It would appear that, contrary to previous suggestions, the claims as to the effect of cultivation and "domestication" of rubber resulting from its use as a food, while plausible on the surface, are unwarrantably sweeping and their soundness suspect. It is altogether probable that man has had little, if any, appreciable influence on the overall course of evolution in the genus *Hevea*.

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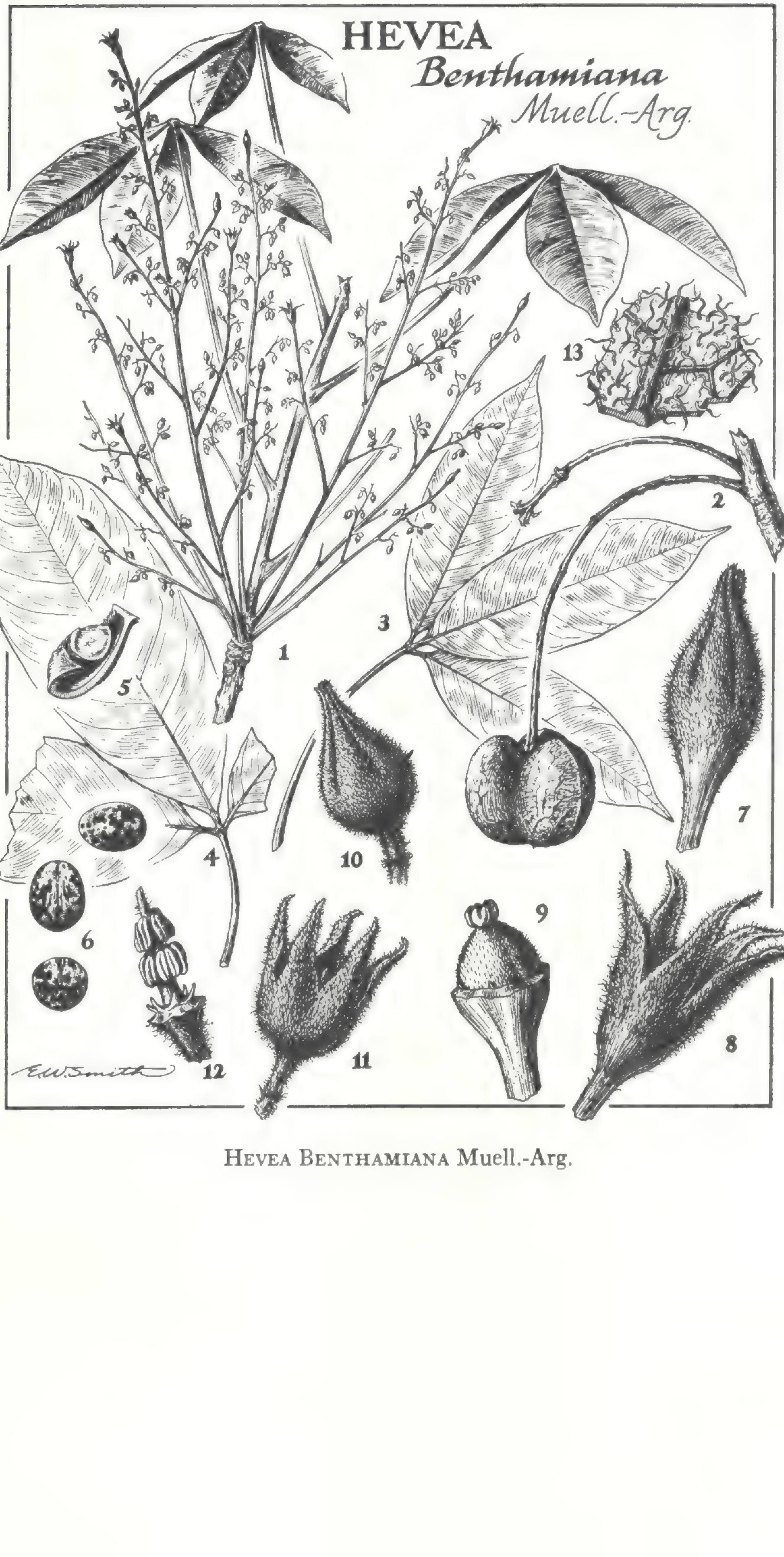
EXPLANATION OF PLATES

PLATE I. *Hevea Benthamiana* Muell.-Arg. 1) Flowering branch, about ½ natural size; 2) Fruiting branch, about ½ natural size; 3 and 4) Leaf variations, about ½ natural size; 5) Valve of capsule, about ½ natural size; 6) Seeds, about ½ natural size; 7) Pistillate bud, about 5 × natural size; 8) Pistillate flower, about 5 × natural size; 9) Ovary with calyx removed, about 7½ × natural size; 10) Staminate bud, about 5 × natural size; 11) Staminate flower, about 5 × natural size; 12) Staminal column with calyx removed, about 7½ × natural size; 13) Section of under surface of leaf, about 7½ × natural size.

PLATE II. *Hevea nitida* Muell.-Arg. 1) Flowering branch with young leaves, about ½ natural size; 2) Fruiting branch, about ½ natural size; 3) Leaf variations, about ½ natural size; 4) Valve of capsule, about ½ natural size; 5) Seeds, about ½ natural size; 6) Staminate bud, about 5 × natural size; 7) Staminate flower, about 5 × natural size; 8) Staminal column with calyx removed, about 7½ × natural size; 9) Pistillate flower, about 5 × natural size; 10) Pistillate bud, about 5 × natural size; 11) Ovary with calyx removed, about 7½ × natural size.

PLATE III. *Hevea nitida* Muell.-Arg. var. *toxicodendroides* (Schult. & Vinton) R. E. Schultes. 1) Flowering branch, about ½ natural size; 2) Fruiting branch, about ½ natural size; 3 and 4) Leaf variations, about ½ natural size; 5) Valve of capsule and seeds, about ½ natural size; 6) Staminate bud, about 5 × natural size; 7) Staminate flower, about 5 × natural size; 8) Staminal column with calyx removed, about 7½ × natural size; 9) Pistillate flower with one calyx lobe removed, about 5 × natural size; 10) Pistillate bud, about 5 × natural size; 11) Ovary with calyx removed, about 7½ × natural size.

PLATE IV. *Hevea rigidifolia* (Spruce ex Benth.) Muell.-Arg. 1) Flowering branch, about ½ natural size; 2) Leaf variations, about ½ natural size; 3) Valve of capsule, about ½ natural size; 4 and 5) Seed, about ½ natural size; 6) Pistillate bud, about 5 × natural size; 7) Pistillate flower, about 5 × natural size; 8) Ovary with calyx removed, about 7½ × natural size; 9) Staminate bud, about 5 × natural size; 10) Staminate flower, about 5 × natural size; 11) Staminal column with calyx removed, about 7½ × natural size.



HEVEA BENTHAMIANA Muell.-Arg.

HEVEA NITIDA Muell.-Arg.

HEVEA *nitida* Muell.-Arg.
var. **toxicodendroides**
(Schult. & Vinton) R.E. Schult.

HEVEA NITIDA Muell.-Arg. var. TOXICODENDROIDES (Schult. & Vinton) Schultes

HEVEA RIGIDIFOLIA (Spruce ex Benth.) Muell.-Arg.

STUDIES IN THE THEACEAE, XXVIII
MELCHIORA, A NEW GENUS IN AFRICA

Clarence E. Kobuski

Approximately ten years ago while reviewing the genus Adinandra [1] I was both impressed and intrigued by the presence of two unusual species quite isolated in Africa and far removed from the Asiatic-Malaysian taxa of the genus. Furthermore, these two African species were two thousand miles distant from each other. One, *Adinandra mannii* Baker, obviously a very rare species, has been found only on the tiny island of St. Thomas, close to but off the western coast of Africa in the Gulf of Guinea. The second species, *A. schliebenii* Melchior, was described from material collected near the eastern coast of Africa in the Territory of Tanganyika, separated from the first species by the span of the complete continent. In 1950, three years after my paper on *Adinandra* had been published, a third species *A. intermedia* Boutique & Troupin was described from Belgian Congo, Uganda and the Territory of Tanganyika. While having many fundamental characteristics of the genus *Adinandra* these three taxa have several distinct features which clearly set them apart.

Szyszylowicz (1893) in his treatment of the family for Die Natürliche Pflanzenfamilien recognized in the one African species (*A. mannii*) described at that time enough differences to establish a new section Eleutherandra based primarily on the free stamens in the flower. Two other sections were introduced at the same time. The three sections were as follows:

Sect. I. Eleutherandra: Stamens free

Sect. II. Euadinandra: Stamens in bundles

Sect. III. Symphiandra: Stamens joined and disposed in a tube

Later, in 1925, Melchior continued the use of these sections but added a fourth, Eleutherostyla, separating his new section from those of Szyszylowicz on the basis of the free styles. This last section of Melchior is now the New Guinea genus *Archboldiodendron*. At the time of his treatment Melchior stated that the knowledge of the stamens was too incomplete to group the species by sections, especially in Sections II and III, which comprise the Asian-Malaysian species and as a result treated all the species geographically. I found it expedient to follow Melchior's method of treatment for two reasons. In the first place, except for the taxa *A. millettii* (China) and *A. dumosa* (Malaysia) the species are endemics of very limited range. Secondly, eight out of every ten specimens of *Adinandra* have been collected in the fruiting stage and many taxa have been described from the fruit alone. Furthermore, it is difficult, in working with

[1] Studies in the Theaceae, XV. A review of the genus Adinandra. Jour. Arnold Arb. 28: 1–98. 1947.

herbarium material, to place a species definitely in its respective section even with the stamens present.

The second species of the African section Eleutherandra, *A. schliebenii*, was described by Melchior in 1934. In this treatment Melchior gave a very interesting and enlightening discussion of the species, quoting excerpts from a letter written by the collector, H. J. Schlieben and contrasting the new taxon with *A. mannii* described sixty-six years earlier.

Besides the free stamens used as a means of separating these three species from the other taxa in *Adinandra* there are other features of importance which set them apart and which taken together form a group worthy of generic distinction.

The features of distinction are as follows: (1) Stamens few, in a single series, the filaments glabrous and free except at the very base, the anthers glabrous (without setae) and subsagittate; (2) Corolla-lobes orange and red, three times longer (35–50 mm.) than the calyx-lobes, connate at the base only, otherwise free, disposed in a pseudo-tube, the apices of the lobes arching over the pistil and stamens.

The feature of relationship with *Adinandra* is found in the fruit. The indehiscent capsules are 4-celled, incompletely 5-celled or 5-celled, with many small, reniform, shiny seeds. The placentae are bifid.

It is a pleasure to name this new genus *Melchiora* for Professor Hans Melchior of the Botanisches Museum at Berlin-Dahlem, Germany. For years Professor Melchior has shown a continued interest in and has made many valuable contributions to our knowledge of the family Theaceae. The section name Eleutherandra is not available for generic use since it has been used by Van Slooten (1925) for a genus in the Flacourtiaceae. Another name, *Adinandropsis* has been published as a *nomen nudum*.

Melchiora, gen. nov.

Adinandropsis Pitt-Schenkel in Jour. Ecol. **26**: 80. 1938, nom. nud.

Arbores. Folia alternata, simplicia, chartacea vel subcoriacea, penninervia. Flores hermaphroditi, in axillis foliorum solitarii; bracteolae duae, persistentes; sepala quinque, imbricata, concava, persistentia, crassa inaequalia, exteriora satis breviora; petala quinque, libera; stamina uniseriata, pauca (15–35), filamentis filiformibus, glabris, liberis (inter se), basi ad corollam adnatis, antheris glabris (sine setis), basi cordato-sagittatis, apice apiculatis; ovarium quattorloculare, vel quinqueloculare, multiovulatum, placenta in quoque loculo bifida, stylo filiformi, stigma leviter quinquesulcatum. Fructus indehiscens, in sicco subligneus, sepalis bracteolisque persistentibus. Semina in quoque loculo multa, parva, reniformia, testa brunnea, nitida, reticulata.

TYPE SPECIES: *M. mannii* (*Adinandra mannii* Baker).

KEY TO THE SPECIES

Young branchlets tuberculate-punctate; leaves subrotund at the base; ovary 4-celled, glabrous; style glabrous. *M. mannii.*

Young branchlets smooth; leaves cuneate at the base; ovary 5-celled, sericeous; style sericeous on lower portion, glabrous upper part.

Petals acute and entire at the apex; the inner three sepals sericeous on the dorsal surface, the outer two glabrous; stamens 15–20. . . . . *M. schliebenii.*

Petals obtuse or rounded and denticulate at the apex; all sepals glabrous without, sericeous within; stamens 25–35. . . . . *M. intermedia.*

Melchiora mannii (Oliver), comb. nov.

Adinandra mannii Oliver in Fl. Trop. Afr. **1:** 170. 1868. — Hooker, Icon. Pl. **11:** 29, *t. 1039.* 1867. — Szyszylowicz in Nat. Pflanzenfam. III. **6:** 189. 1893. — Melchior in Notizbl. Bot. Gart. Mus. Berlin **8:** 657. 1924; **11:** 1100. 1934; in Nat. Pflanzenfam. ed. 2. **21:** 144. 1925. — Exell, Cat. Vasc. Plts. S. Tomé 112. 1944. — Kobuski in Jour. Arnold Arb. **28:** 94. 1947. — Boutique & Troupin in Bull. Jard. Bot. Bruxelles, **20:** 65. 1950.

DISTRIBUTION: West Africa (Island of St. Thomas).

ISLAND OF ST. THOMAS: summit of the peak on the island, *G. Mann 1066* (ISOTYPE, GH).

Tree 10 m. high; branches gray, terete, glabrous, the young branchlets red-brown, glabrous, terete, minutely tuberculate-punctate, the terminal buds glabrous. Leaves chartaceous to subcoriaceous, oblong-elliptic to oblong-obovate, quite uniform in size, 6–7 (–9) cm. long, 2–3 cm. wide, acuminate at the apex, asymmetrical, subrotund at the base, glabrous on both surfaces, the midrib reddish near the base, tuberculate-punctate on the lower surface, the margin glandular-denticulate, the veins 15–18 pairs, conspicuous but not prominent, anastomosing midway to the margin, the petiole 1–2 mm. long. Flowers axillary, ? solitary; pedicel ca. 2 cm. long (fide Oliver), glabrous; bracteoles 2, persistent, glabrous, opposite, immediately below the calyx, broadly ovate, 7–8 mm. long, 5–6 mm. wide, acute at the apex, carinate; calyx-lobes 5, imbricate, glabrous on the exterior surface, very lightly appressed-pubescent (with binocular) on the interior surface, broadly ovate, acute at the apex, unequal, the two outer lobes 12–14 mm. long, ca. 10 mm. wide, the three inner lobes 17–19 mm. long, ca. 10 mm. wide, their inner margins scarious, entire; corolla-lobes 5, slightly connate only at the very base, not spreading, somewhat tubuliform, oblong, ca. 25 (35–45) mm. long, 7–10 mm. wide, obtuse to subrotund at the apex; stamens ca. 30 in a single series, equal, ca. 10 mm. long, the filaments glabrous, ca. 6 mm. long, adnate to the base of the corolla, otherwise free, the anthers oblong-linear, ca. 4 mm. long, strictly glabrous, the apicule less than 0.5 mm. long, truncate to emarginate; ovary conical-ovoid, glabrous, ca. 4 mm. diam., tapering into the style, 4-celled, multi-ovulate, the placentae bifid, the style glabrous, entire, ca. 22 mm. long, the stigma 4-lobed. Fruit not seen.

An examination of the isotype in this species shows that the ovary is distinctly 4-celled. A 4-celled ovary is unusual in the Theaceae. However, in *Adinandra* two species, *A. myrioneura*, of British North Borneo, and

A. oblonga, of Siam, have 4-celled ovaries with innumerable small ovules, like that found in this species.

One might expect, from an examination of more material of the species, to find specimens in which the ovary is 5-celled as in *M. intermedia*. According to Exell, however, the species may be no longer in existence. In his Catalogue of the Vascular Plants of S. Tomé (p. 113. 1944) he states: "I made a hasty search for *A. Mannii* on the Pico in November 1932, but without success. A tremendous rainstorm was in progress and one could see only a few yards. The vegetation near the summit of the Pico has been partially cleared and some *Cinchona* planted, so that it is possible that *A. Mannii* is now extinct. It was last collected by Campos in 1907."

There are other isolated species in the Theaceae that have suffered a like fate. *Freziera cordata* Tulasne, known only from Martinique, was obliterated in the devastating volcanic eruption of Mt. Pelée on that island in 1902. *Franklinia alatamaha* Marshall, found only in Georgia near Fort Barrington in McIntosh County, was last collected in the late eighteenth century. This species was probably exterminated as a spontaneous plant in the years 1787 and 1789 by nurserymen in an effort to fill large orders for the species for a London firm.

Melchiora schliebenii (Melchior), comb. nov.

Adinandra schliebenii Melchior in Notizbl. Bot. Gart. Mus. Berlin **11**: 1076, 1097. 1934. — Kobuski in Jour. Arnold Arb. **28**: 95. 1947. — Boutique & Troupin in Bull. Jard. Bot. Bruxelles, **20**: 65. 1950.

DISTRIBUTION: East Africa (Tanganyika Territory).

TANGANYIKA TERRITORY: Uluguru, in fog forest northwest side of Lupanga Mountains; tree 20–30 m., flowering and fruiting, with orange and red flowers, *H. J. Schlieben 3175*, (ISOTYPE, AA), December 28, 1932.

Tree 20–30 m. high; very young branchlets smooth, compressed, glabrous, red to gray-brown. Leaves chartaceous to coriaceous, obovate-oblong, 5–10 cm. long, 2–3.5 cm. wide, acute at the apex or shortly and obtusely acuminate, cuneate at the base, glabrous on both surfaces, the midrib red beneath, the margin serrulate-dentate, glandular, the veins conspicuous beneath because of the red color, the petiole ca. 5 mm. long. Flowers axillary, solitary, ca. 3 cm. long; pedicels 2.5–3.5 cm. long, recurved, glabrous; bracteoles 2, persistent, opposite, immediately below the calyx, glabrous, broadly ovate, acute at the apex, carinate, the outer one 3 mm. long and wide, the inner one 5 mm. long and wide; calyx-lobes 5, imbricate, ovate, acute at the apex, unequal, varying in length from 10 mm. (outer lobe) to 17 mm. (inner lobe), ca. 12 mm. wide, the two outer lobes glabrous on the exterior surface, the three inner lobes sericeous on the exterior surface except along the scarious margins, ciliolate; corolla-lobes 5, free, twice as long as the innermost calyx-lobe, linear-oblong, 32–45 mm. long, 5–7 mm. wide, acute at the apex, somewhat narrowed and connate at the base, not spreading, somewhat tubuliform; stamens 15–20, uni-

seriate, ca. 15 mm. long, glabrous, the filaments free (inter se), adnate to the base of the corolla, filiform, 8–9 mm. long, the anthers linear, ca. 5 mm. long, cordate-sagittate at the base, the connective projected at the apex into a small subulate-lanceolate apicule 1 mm. long; ovary conical, ca. 6 mm. long, 4 mm. diam., sericeous-tomentose, imperfectly 5-celled, multi-ovulate, attenuate at the apex into a filiform style 24–30 mm. long, sericeous along the lower portion, glabrous along the upper portion, lightly 5-sulcate, the stigma minute, lightly 5-sulcate. Fruit indehiscent, conical-ovoid, ca. 2 cm. long, 1 cm. diam., the seeds many, small, reniform, 1.2–1.5 mm. diam., brown, shiny, reticulate.

Whereas *Melchiora mannii* has been shown to have been a rare species of very limited geographical range, *M. schliebenii* is known to enjoy a well-established stand in Tanganyika Territory. Quoting from a letter by the collector (H. J. Schlieben), Melchior records a stand of many trees and that the species seems to flower throughout the year. He mentions that on the east side of Magali Mountain (alt. 2450 m.), seventy percent of the trees are of this species. The trees are severely forked at this altitude. He also states that the heartwood is very hard and red in color.

There are other instances in the family Theaceae in which species are known to dominate isolated areas. On the tabletop mountains in Venezuela three species of *Bonnetia* are sufficiently abundant to form what are known as "Bonnetia forests." On Ptari-tepuí one finds *B. steyermarkii* forming impenetrable thickets and also mixed with *B. roraimae* in "Bonnetia roraimae forests." *Bonnetia sessilis* is the dominant species on the mesa between Ptari-tepuí and Sororopan-tepuí. All of these species, although abundant, are strict endemics.

Melchiora intermedia (Boutique & Troupin), comb. nov.

Adinandra intermedia Boutique & Troupin in Bull. Jard. Bot. Bruxelles, **20**: 62. 1950.
Adinandropsis, sp. nov. Pitt-Schenkel in Jour. Ecol. **26**: 80. 1938, nom. nud.

DISTRIBUTION: Belgian Congo, Uganda, Tanganyika Territory. — Fide Boutique & Troupin.

NO SPECIMENS EXAMINED.

Trees erect, up to 40 m. high; branchlets glabrous, leaves generally disposed at the ends of the branchlets, chartaceous to submembranaceous, elliptic, oblong-elliptic or obovate, 7–13 (–18) cm. long, 2–4 (–6) cm. wide, acute or shortly acuminate at the apex, cuneate at the base, glabrous on both surfaces, green above, pale or yellow-green below, the midrib sulcate above, somewhat prominent beneath, the secondary nerves 17–20, red, the margin serrulate-dentate, the petiole ca. 5 mm. long. Flowers axillary, solitary, 3.5–5 cm. long; pedicel 1–3 cm. long, glabrous; bracteoles 2, persistent, unequal, suborbicular, often subacute at the apex, the outer one 2–4 mm. long and wide, the inner one 7–9 mm. long and wide; calyx-lobes 5, imbricate, unequal, 1.5–3 cm. long, 1.2–1.6 cm. wide, the outer one

often subrotund at the apex, the others acute at the apex, glabrous externally, sericeous within; corolla-lobes 5, free, glabrous, erect, slightly connate at the base, somewhat tubular, 3.5–5 cm. long, 5–7 mm. wide, obtuse to rounded and denticulate at the apex; stamens 25–35, uniseriate, 11–16 mm. long, glabrous, the filaments free, filiform, 6–8 mm. long, lightly adnate to the base of the corolla, the anthers linear, cordate-sagittate, 5–8 mm. long, the connective projected at the apex into a small subulate-lanceolate apicule 0.7–1.5 mm. long; ovary conical, 5–10 mm. long, 3–6 mm. across, sericeous-tomentose, 5-celled, multi-ovulate, alternate at the apex into a filiform style 3–5 cm. long, sericeous along the lower portion, glabrous toward the apex, the stigma minute, lightly sulcate. Fruit indehiscent, conical-ovoid, 2–3 cm. long, ca. 1 cm. across, the seeds many, reniform or discoid, ca. 1 mm. diam., reticulate.

Unfortunately, none of the four specimens cited by Boutique & Troupin has been available for this study. However, in preparing an English description, I was impressed by the great similarity between *M. intermedia* and the earlier species, *M. schliebenii* described by Melchior.

The apex of the corolla-lobes is described as obtuse to rotundate and denticulate. As illustrated in the original publication, this denticulation appears very distinctive. Another character, the absence of pubescence on the external surface of the inner lobes of the calyx also distinguishes the species from *M. schliebenii*.

The other differences of importance appear to be those of size. I list below a comparison of these sizes as found in the two taxa *M. schliebenii* and *M. intermedia*. One will observe that there is greater variation listed for *M. intermedia* than for *M. schliebenii*. It is also obvious that in these two taxa the listed measurements are equal or overlap. Probably the reason is because Boutique & Troupin had four specimens from which to draw their conclusions while Melchior described his species from a single specimen.

	M. schliebenii	*M. intermedia*
HABIT:	Tree 20–30 m. high; severely forked	Trees to 40 m. high; erect
LEAVES:	5–10 cm. long; 2–3.5 cm. wide	7–13 cm. long; 2–4 cm. wide
PETIOLE:	5 mm. long	5 mm. long
PEDICEL:	2.5–3.5 cm. long	1–3 cm. long
BRACTEOLES:	outer: 3 mm. long & wide inner: 5 mm. long & wide	outer: 2–4 mm. long & wide inner: 7–9 mm. long & wide
SEPALS:	10–17 mm. long, 12 mm. wide	15–30 mm. long, 12–16 mm. wide
PETALS:	32–45 mm. long, 5–7 mm. wide	35–50 mm. long, 5–7 mm. wide
FILAMENTS:	8–9 mm. long	6–8 mm. long
ANTHERS:	5 mm. long	5–8 mm. long
CONNECTIVE:	1 mm. long	1 mm. long
OVARY:	6 mm. long, 4 mm. diam.	5–10 mm. long, 3–6 mm. diam.
STYLE:	24–30 mm. long	30–50 mm. long

The distribution of *M. intermedia* as recorded by the authors appears to be far more extensive than that of the other two taxa. In fact, it almost invades the area recorded for *M. schliebenii*, since it has been recorded from Usambara (*Pitt-Schenkel 376*) in the Territory of Tanganyika, a locality only a little more than a hundred miles north along the coast from the type locality of *M. schliebenii*.

Another interesting comparison is that Schlieben, the collector of *M. schliebenii*, records his material as coming from an area in which the tree is the dominant element of the flora. Michelson, the collector of the type of *M. intermedia*, also records his specimen as coming from an area in which this species is the dominant element.

It sems that in the case of these two species, both dominating the flora of rather extensive localities which perhaps overlap, an opportunity to make a population study of the taxa in the woody family Theaceae may be afforded. This is indeed a rare opportunity, since the species in this family are usually isolated indigens and are seldom found growing abundantly or in close enough proximity to warrant such a study. Considering the great variation found within the taxa of this family, further study of ample material may show *M. schliebenii* and *M. intermedia* to constitute a single variable species.

A TAXONOMIC REVISION OF PODOCARPUS
X. THE SOUTH PACIFIC SPECIES OF SECTION EUPODOCARPUS, SUBSECTION D

NETTA E. GRAY *

THE SPECIES AND VARIETIES of *Podocarpus* in subsection D of section *Eupodocarpus* are: *Podocarpus totara* D. Don, *P. hallii* Kirk, *P. nivalis* Hooker, *P. nivalis* var. *erectus* Cockayne, *P. acutifolius* Kirk, *P. alpinus* R. Brown, *P. gnidioides* Carrière and *P. nubigenus* Lindley. All of these are found in southern regions of the Pacific Ocean. Of the species growing in the southwest, all are found on the large islands: New Zealand, New Caledonia and Tasmania. *Podocarpus alpinus*, on Tasmania, is also found in the southeastern part of the continent of Australia. *Podocarpus nubigenus* is the only one of these species growing on the American side of the Pacific; it is found in the mountainous regions of southern Chile and, incidentally, has the southernmost range of any podocarp. Orr (15), using only geographical groups in the section *Eupodocarpus*, discussed *P. gnidioides* and *P. nubigenus* as exceptions in their areas. However, in his discussion of the New Zealand members, he emphasized the similar characteristics of all of them. The interesting distribution of these species, in the southern parts of South America and Australia and in New Zealand, is also found in other groups of plants and is considered when theories of land bridges or continental drift are under discussion (2).

Podocarpus totara, *P. hallii* and *P. nubigenus* are the only species with tree habit and large enough to be of some use in industry. *Podocarpus acutifolius* and *P. nivalis* var. *erectus* are erect but shrubby. *Podocarpus gnidioides*, *P. alpinus* and *P. nivalis* are low shrubs often having prostrate or decumbent branches. They are all small-leaved, exceeding 2 cm. in length only in *P. hallii* and *P. nubigenus* and exceeding 3.5 mm. in width also in *P. totara*. The small, crowded leaves, together with the low shrubby nature of several of the species, make the taxoid appearance of these plants quite apparent. The ridges on the twigs, formed by the decurrent petioles, are less prominent in *P. totara* and *P. hallii* and the leaves are not so densely crowded.

In the leaf anatomy one can see that these species belong in section *Eupodocarpus*. Some of the characters in common with other members of this section are a single midvein, stomata only on the lower surface, varying amounts of hypoderm on both sides and palisade mesophyll only on the upper side of the leaf.

* The author wishes to express her appreciation to Prof. A. Guillaumin of the Paris Museum Herbarium for permission to examine critical specimens. She wishes to acknowledge the assistance of the late Prof. John T. Buchholz in the interpretation of specimens from New Caledonia and the examination of those in the Paris Museum Herbarium. She thanks also Dr. H. W. Rickett of The New York Botanical Garden for special interpretation of the International Code of Botanical Nomenclature.

All of these species differ in their leaf anatomy from the rest of section *Eupodocarpus* by the absence of an organized accessory transfusion tissue. The lignified elements in the mesophyll, representing the accessory transfusion tissue, show variation both in the degree of lignification of single cells and in the number of cells in which the walls are so thickened. Juvenile and young leaves may not show any thickening of mesophyll cell walls, while mature leaves from exposed situations and from fruiting branches may have adjacent cells extending from the vascular transfusion tissue to the margin of the blade of the leaf. *Podocarpus gnidioides* shows these cells loosely arranged in a tissue (15, pl. 2, fig. 6) but they can scarcely be said to be oriented transversely to the blade of the leaf as in *P. totara*. Among these species, *P. gnidioides* has the most thickening and *P. acutifolius* the least. These lignified elements resemble those of section *Afrocarpus* rather than typical accessory transfusion tissue. Griffin (12) made a study of their development in *P. totara* and regarded them as belonging to true accessory transfusion tissue. However, Orr (15) speaks of this as a "misnomer" and considers them only as strengthening units similar to the lignified, pitted cells found in the mesophyll and palisade of section *Eupodocarpus* subsections A, B and C, rather than conducting elements even though here in subsection D they have not been found in either of the mentioned positions. Entertaining Orr's view, subsection D would not have accessory transfusion tissue. A dual role, conduction and support, is usually understood for lignified, pitted elements in vascular tissues. It hardly seems necessary in this case to ascribe one of these functions to auxiliary sclereids for all species to the complete exclusion of the other. Certainly even transversely oriented parenchyma cells also serve in conduction. These cells with thickened walls, regardless of number, often retain protoplasmic substances. The cells derive their origin from differentiating mesophyll whether they are true organized accessory transfusion tissue, isolated sclereids in the same location in the leaf, or auxiliary sclereids among or adjacent to the palisade tissue. This has very recently been observed by Griffith (13) while studying the ontogeny of vascular transfusion tissue in *Podocarpus macrophyllus*. A review of the literature relating to accessory transfusion tissue is to be found in Orr (15).

The single resin canal beneath the phloem varies considerably in size. It seems to be consistently small in *Podocarpus acutifolius*, large in *P. nivalis*, *P. gnidioides* and *P. alpinus*, but in *P. totara* and *P. hallii* it is found to vary from half the width of the vascular bundle to fully as wide.

The hypodermal fibers are mostly small. In *Podocarpus totara*, *P. hallii*, *P. nivalis* and *P. alpinus* they vary from 17–25μ in diameter, seldom more than 15μ in *P. acutifolius*, and often more than 30μ in *P. gnidioides*. They are arranged in a single upper layer except at the margins in *P. acutifolius*. The layer is sometimes doubled and usually is interrupted in *P. alpinus* and *P. nivalis*, but mostly continuous in *P. totara* and *P. hallii*. Hypodermal fibers are found between the stomatal rows in all species but *P. gnidioides* and are most abundant in *P. totara* and *P. hallii*.

True fibers between the phloem and the resin canal were found in several leaves of *Podocarpus totara* and *P. alpinus*. Such fibers, however, are exceedingly rare in this subsection. In some of the other species, the mesophyll cells surrounding the vascular bundle seem to be differentiated in having denser cell contents or slightly thickened walls, but never by being enlarged.

The species in this group do not have bracts on the peduncle of the female cone below the receptacle, suggesting a closer relationship to subsection C in South America than to those species in the western south Pacific region. The single resin canal beneath the phloem is also characteristic of both subsections. Pilger (17) divides section *Eupodocarpus* into two subsections, A and B. In his subsection A he groups all the American species of *Eupodocarpus* and the species included in subsection D in this study.

Concentrated studies on the New Zealand conifers have been made and the polymorphism of many of them led to the early recognition and study of hybridization in the wild flora. This was found to account for the intergrading varieties between *Podocarpus totara* and *P. hallii*, two large trees, by Cockayne (6) and *P. hallii* and *P. nivalis*, a tall tree and a depressed shrub. A likely result of the latter cross may be *P. nivalis* var. *erectus* which has not yet been recognized as a hybrid. The former was named *P.* × *loderi* by Cockayne, but he considered it too early to present a definite name for the latter.

This subsection of *Eupodocarpus* has had the most extensive investigation of chromosome number (18). *Podocarpus acutifolius*, *P. alpinus* and *P. nivalis* agree with the other members of section *Eupodocarpus* in having n = 19. Burlingame is quoted as saying *P. hallii* has n = 12 but this bears reinvestigation as other counts made by this author have been incorrect.*

The taxonomy of *Podocarpus nubigenus* is not repeated in this paper as it was included with the species of section *Eupodocarpus* from South America (3).

KEY TO THE SPECIES OF SECTION EUPODOCARPUS, SUBSECTION D

Leaves pungent-mucronate; trees or shrubs.
- Leaves 1–4 cm. (rarely 6 cm.) long; trees.
  - Leaves 2–3.5 mm. broad; bark thick; male flowers rarely solitary, subsessile; seed obtuse . . . . . *P. totara.*
  - Leaves 3–6.5 mm. broad; bark papery; male flowers solitary, peduncled; seed acute . . . . . *P. hallii.*
- Leaves 0.6–2.5 cm. long; shrubs.
  - Leaves thick, coriaceous; hypoderm interrupted; resin canal large.

* A recent communication from Dr. J. B. Hair, Crop Research Division, New Zealand, indicates that the chromosome counts of several of these species, when taken from native material, differ from the counts quoted above. He finds that the 2n chromosome number is 34 for *P. totara*, *P. hallii*, and *P. acutifolius*, 38 for *P. nivalis* and 36 for *P. nivalis* var. *erectus*.

Prostrate branches; leaves not over 1.5 cm. long. . . . . *P. nivalis.*
Erect branches; leaves up to 2.5 cm. long . . . . . *P. nivalis* var. *erectus.*
Leaves thin, coriaceous; hypoderm continuous; resin canal small. . . . . *P. acutifolius.*
Leaves obtuse or rotundate at apex, not pungent; shrubs.
Upper midrib of leaves flattened; pollen cones facicled 3–6; hypoderm interrupted, single layer, fibers small . . . . . *P. alpinus.*
Upper midrib sulcate; pollen cones solitary; hypoderm continuous, doubled, fibers large . . . . . *P. gnidioides.*

Podocarpus totara D. Don ex Lamb. Pinus ed. 2, 189. 1832; A. Cunn. in Ann. Nat. Hist. 1: 212. 1838 (excl. synon.); D. Don ex Hooker in Lond. Jour. Bot. 1: 572. 1842; Raoul, Choix Pl. Nouv. Zél. 41. 1846; Endlicher, Syn. Conif. 212. 1847; Hooker f., Fl. Nov. Zealand 1: 233. 1853, Handb. N. Z. Fl. 258. 1864; Gordon, Pinetum 285. 1858, ed. 2, 350. 1875; Carrière, Traité Conif. ed. 2, 652. 1867 (excl. var.); Parlatore in DC. Prodr. 16: 514. 1868; Bertrand in Ann. Sci. Nat. ser. 5, 20: 59. 1874; Mahlert in Bot. Centralbl. 24: 280. 1885; Kirk, Fl. N. Zealand 227. 1889; Kent in Veitch's Man. Conif. 153. 1900; Van Tieghem in Bull. Soc. Bot. France 38: 169. 1891; Pilger in Pflanzenreich **IV. 5**(Heft 18): 84. 1903, in Nat. Pflanzenfam. ed. 2, 13: 248. 1926; Cheeseman, Man. New Zealand Fl. ed. 1, 638. 1906, ed. 2, 111. 1925; Griffin in Trans. N.Z. Inst. 40: 43. 1907; Cockayne, Veg. N. Z. in Engler & Drude, Veg. der Erde, *t. 28.* 1921, *t. 22.* 1928; Bailey, Cult. Evergreens 180. 1923; Dallimore & Jackson, Handb. Conif. 56. 1923, 1931, 83. 1948; Florin in Svenska Vet.-Akad. Handl. ser. 3, 10: 280. 1931; Laing & Blackwell, Pl. of N. Z. ed. 4, 66. 1940.

Podocarpus bidwillii Hoibrenk in Endlicher, Syn. Conif. 213. 1847.

Podocarpus cunninghamii Colenso, Visit to Ruahine Range 58. 1844.

A large tree, 10–30 m. or more high, trunk 0.5–2 m. in diameter, with thick bark; the short, sometimes thickly leafy branchlets scattered or subverticillate, green, scarcely ridged. Terminal buds 1.2–1.5 mm. wide, globose or ovate, with 2 series of bud scales usually sharply differentiated, the outer scales lanceolate, sometimes foliaceous, up to 3 mm. long, acute, attenuate, tips usually divaricate, green; inner imbricate, curving over growing tip, apiculate, ovate, brownish, margins scarious and erose. Leaves spreading scattered or arranged in 2 rows, 1–2 cm. long, 2.5–4 mm. wide, linear, rigid and coriaceous, very thick, pungent, narrowed at both ends, sharply pointed, straight or curved, sessile (juvenile leaves not essentially different); midrib not evident or only shallowly impressed above, clearer beneath. Pollen cones axillary, subsessile, fascicled 2 or 3, or at end of a short thick peduncle 1–2 mm. long (rarely solitary according to Kirk), base surrounded by stiff broad scales, erect, cylindrical, 1.5 cm. long, 3 mm. broad. Microsporophylls closely imbricate, rhomboidal, with a short obtuse apiculus, scarious margined, and sparingly denticulate. Female cones solitary, axillary, on short peduncles 2–3 mm. long; recep-

tacle of 2–4 fused fleshy scales, the upper ones not well developed, free at tip, subglobose and red when mature. Seeds 1 or 2 but usually solitary, small, subglobose, obtuse or rounded at apex, 10–12 mm. long.

DISTRIBUTION: New Zealand, on both North and South Islands, on slopes from sea level to 650 m., reaching largest size at 400 m. altitude. Not on Stewart Island.

In 1889, Kirk (14) distinguished *Podocarpus totara* from his new species, *P. hallii*, morphologically and geographically. In the former species the branchlets are always stiff and rigid, even in immature plants; the leaves do not differ in the young state from the mature leaves, the sessile male cones are rarely solitary and the seed is rounded at the apex and usually solitary. Thus he restricted the description somewhat from that of Pilger (16) which was written to include both species. In a short summary differentiating these two species, Kirk seems to have erred by reversing the mature leaf size which, for *P. totara*, is smaller in most cases, rarely exceeding 2 cm. in length and only reaching 3 mm. in width.

The cultivated specimen at Kew, known as *Podocarpus totara*, has rigid leaves which taper gradually toward the apex and suggest that it may rather be *P. hallii*, or a hybrid. *UC10423*, collected by Setchell in 1904, was determined by Cheeseman as *P. totara*, but it exceeds all specimens of this species seen in the size of the leaves.

There has been some minor confusion in the form of the name and its source. Don (10) first used the native name Totara to designate the species in 1832. Cunningham again described it in 1838 (8), calling it *Podocarpus totara*, the form used by New Zealand authorities Cockayne (6), Cheeseman (5), Kirk (14), and Pilger (17). The name is sometimes credited to A. Cunningham, but, following the International Code, it should be to D. Don as the earliest publication of the name.

SPECIMENS EXAMINED: *

NEW ZEALAND: North Island: Whangarei, *Kirk s.n.* (A, †F, †Mo, UC), *Kirk s.n.* (GH), *McLeod* in 1913 (†UC), *Cunningham 328* (TYPE) (†BR, K), Ruatangata, *Gordon* in 1910 (K–4 sheets); Bay of Islands, *Capt. Home s.n.* (†BM); *Matthews* in 1905 (†UC); Wellington, *Lawton s.n.* (†Ill). South Island: Otira Luga, *Kirk 467* (GH); Canterbury, *Adams* in 1914 (A); Woodbury, *Meebold 4059* (NY); Dunedin, *Meebold 4257* (NY); Mt. Martii, *Haast* in 1866 (†BR); Waya-runa Bay, U.S. So. Pac. Expl. Exped., *Anon.* in

* The following symbols indicate the herbaria of the specimens cited: Academy of Natural Sciences of Philadelphia (Ph), Arnold Arboretum (A), British Museum (BM), Brussels Botanical Garden (BR), University of California at Berkeley (UC) and at Los Angeles (LA), California Academy of Science (CAS), Chicago Natural History Museum (Field Museum) (F), Cornell University (CU), Gray Herbarium (GH), University of Illinois Herbarium (Ill), Royal Botanic Gardens, Kew, (K), Missouri Botanical Garden (Mo), New York Botanical Garden (NY), Paris Museum National d'Histoire Naturelle (P), Yale University Herbarium (YU).

† This symbol preceding the abbreviated name of an herbarium following the specimens examined signifies that the details of the leaves of this specimen have been examined in cross-section.

1838 (GH). LOCALITY NOT INDICATED: *Colenso* 1631 (K), *Colenso* for J. D. Hooker (K), *J. D. Hooker* (K), *Colenso s.n.* (K).

CULTIVATED: Hontika, *Wilson* in 1921 (A); England, Royal Botanic Garden at Kew, *Anon.* in 1857 (†Mo), *Cook* in 1937 (†Ill); Italy, Botanic Garden, Naples, H.13, *Cestai* to Engelmann in 1870 (†Mo–3 sheets). *Anon.* in 1868 (Mo); U.S. California, Golden Gate Park, *Collins* in 1918 (YU), *Eastwood* in 1913 (CAS), in 1914 (A), in 1916 (A–2 sheets, CAS), *Walther* in 1924 (A), *Buchholz* in 1942 (†Ill), Santa Barbara, *Van Rensselaer 1725* (†Ill).

Podocarpus hallii Kirk, Forest Fl. N. Z. 13. 1889; Cheeseman, Man. N. Z. Fl. 648. 1906, ed. 2, 111. 1925; Cockayne, Veg. N. Z. in Engler & Drude, Die Veg. der Erde 111. 1921, 1928; Pilger in Nat. Pflanzenfam. ed. 2, **13**: 247. 1926; Florin in Svenska Vet.-Akad. Handl. ser. 3, **10**: 279. 1931.

Podocarpus totara var. *hallii* (Kirk) Pilger in Pflanzenreich **IV. 5**(Heft 18): 84. 1903; Dallimore & Jackson, Handb. Conif. 57. 1923, 1931, 83. 1948.

A tall tree, 8–20 m. high, 0.5–1 m. in diameter, with thin papery bark; juvenile plants slender, the branchlets at right angles to main axis or often pendulous. Terminal buds slightly larger than twig, all scales broadly ovate, margins scarious and erose, obtuse and sometimes apiculate. Leaves on mature plants 2–4 cm. long, 1.5–3.5 mm. wide, linear, rigid, coriaceous, close-set in several series, erect, pale green when dry, narrowed at base into a very short flat petiole, tips pungent; midrib prominent beneath. Juvenile leaves 2-ranked, larger than mature leaves, 2–6.8 cm. long, 4–5 mm. wide, lanceolate, spreading, often abruptly narrowed at the base and very gradually narrowing to the apex. Pollen cones sessile, solitary (according to Kirk, 14) on distinctly stalked peduncle. Microsporophylls short, broad, apiculate. Female cones solitary on 2–3 mm. long peduncles; receptacle of 2–4 fused fleshy unequal scales free at acute tips, red at maturity, subglobose. Seed acute, pointed at apex, crested, often in 2's, 1–1.2 cm. long.

DISTRIBUTION: Endemic in New Zealand, most abundant on South Island and especially on Stewart Island, sea level to 950 m.

Several times the specific designation has been used in varietal status. Cheeseman (5), after listing it as a species, says "the variety designation might be right but the bark difference is significant." Pilger (16) lists, but questions, *Podocarpus laeta* Hoibrenk as a synonym of *P. totara* var. *hallii*. Endlicher (11) gives the locality for this species as New Holland (Australia) making the combination most improbable, and its correct position cannot be determined without the type specimen.

At the Royal Botanic Gardens, Kew, is an herbarium specimen said to be from a living specimen believed to be a hybrid of *Podocarpus hallii* and *P. nivalis* brought to Kew from Beech Forest, Bealey Valley, N. Z.*

* The living specimen was not seen in 1950 by Prof. Buchholz on his visit to the garden.

SPECIMENS EXAMINED:

NEW ZEALAND: North Island: Ruatangata, *Setchell* in 1904 (†UC–2 sheets); Kartaria, Mongonni Creek, Carse (K); Bay of Islands, U.S. So. Pac. Exped., *Anon.* (GH); Te Aroha, *Chase & Leland 276b* (†Mo); Ruahine Mts., *Tryon s.n.* (A); *Kirk s.n.* (A). South Island: Clinton Valley, *Cockayne 6648*, *Petrie* (NY); Dunedin, Leith Valley, *Lindsey* in 1935 (CU); Westport, *Townson s.n.* (K); Otira Gorge, *Oliver s.n.* (K). Stewart Island: *Cockayne 6661* (†F–2 sheets), *Kirk s.n.* (†F, GH, †Mo). LOCALITY NOT INDICATED: Flea Bay, *Karva* in 1910 (†A); ex Masters Herb., *Anon.* (K); *Morhange s.n.* (†BR); ex Prager Herb., *Anon.* (CAS); *Prince* in 1898 (GH).

CULTIVATED: England, Roy. Bot. Gard., Kew, *Cook* in 1937 (†Ill); Australia, *Hennings* in 1885 (Mo); U.S., California, Greendale, *Anon.* (A); Golden Gate Park, San Francisco, *Eastwood* in 1916 (CAS), in 1917 (CAS), *Walther* in 1921 (CAS), in 1923 (A), in 1924 (A).

Podocarpus nivalis Hooker, Icon, Pl. pl. 582. 1843; Raoul Choix Pl. Nouv. Zél. 41. 1846; Endlicher, Syn. Conif. 214. 1847; Hooker, f., Fl. N. Z. 232. 1853, Handb. N. Z. Fl. 257. 1864; Carrière, Traité Conif. ed. 2, 655. 1867; Parlatore in DC. Prodr. **16**: 519. 1868; Mahlert in Bot. Centralbl. **24**: 280. 1885, Kirk, For. Fl. N. Z. 65. 1889; Pilger in Pflanzenreich **IV. 5** (Heft 18): 85. 1903, in Nat. Pflanzenfam. ed. 2, **13**: 247. 1926; Cheeseman, Man. N. Z. Fl. 649. 1906, 112. 1925; Cockayne, Veg. N. Z. 1921, 1928; Dallimore & Jackson, Handb. Conif. 53. 1923, 1931, 78. 1948; Florin in Svenska Vet.-Akad. Handl. ser. 3, **10**: 279. 1931; Laing & Blackwell, Pl. N. Z. 66. 1940.

Podocarpus montanus Colenso in Trans. N. Z. Inst. **27**: 395. 1895.

A suberect shrub with numerous crowded, rigid branches, 0.5–2.5 m. high in sheltered situations or a low bush with spreading prostrate rigid branches which give off roots from the under surface in more open areas. Branchlets short, thickly leafy, ridged from pulvini at bases of sessile leaves and prominent leaf scars. Terminal buds globose with short greenish, broadly lanceolate, keeled, acute, scarious-margined, erose outer scales; on seedlings more ovate with triangular scales. Leaves vary in size, the larger in the middle of a growth period, thick and coriaceous, very stiff, linear, 0.9–1.5 cm. long, 2–2.5 mm. wide (2.5 cm. long on seedlings), patent, gradually narrowed to base, abruptly obtuse or acute at apex, mucronate, sessile or only very short stalked; midrib prominent below, stout, slightly impressed above giving a folded appearance; margin of blade thickened. Pollen cones fascicled, 2–4 at tip of common peduncle (sometimes solitary according to Dallimore & Jackson, 9), 3–5 mm. long, surrounded at base by minute stiff bracts decurrent on peduncle to leaves, narrowly cylindric, 1 cm. long. Microsporophylls closely imbricated, apiculus scarcely evident. Female cones solitary, axillary, peduncle very short, 1 mm. long, thick; receptacle of two fused fleshy scales free at the obtuse tips, 3–7 mm. long. Seed ovoid, obtusely crested, 5–6 mm. long.

DISTRIBUTION: Endemic on North and South Islands of New Zealand

but not on Stewart Island. Restricted to alpine and subalpine localities, 650–1800 m. altitude.

Podocarpus nivalis is locally known as the Alpine Totara. Its spreading branches are dense and produce a characteristic appearance in the low, thick and often very large amount of ground covered by a single plant.

SPECIMENS EXAMINED:

NEW ZEALAND: North Island: Mt. Ngauruhoe, *Cheeseman s.n.* (K); Ruahine Mts., *Tryon s.n.* (A, †LA); Ruapehu, *Meebold 17905* (NY), ex Masters Herb., *Anon.* (K–2 sheets); *Bidwell s.n.* (†K). South Island: Mt. Movatt, *Kirk 468* (GH); Hooker Valley, Mt. Cook Dist., *Cheeseman 186* (K); Greenstone Valley, Totago, *Haast 49* (K); near Brownings top, *Haast 67* (K); Mt. Whitnomber, *Haast 104* (K); Valley of Camerons near Hawthe Glacier, *Haast 105* (K); on Old Morarius, near Cumuo, *Haast 109* (K); Canterbury, *Haast 541* (K); Mt. Bruce, *Kirk s.n.* (A, †F, †Mo, NY); Arthur's Pass, Southern Alps, *Cockayne 6645* (†CAS, NY); Clarence Valley, *Hector s.n.* (GH); Mt. Martii, *Haast* in 1866 (†BR–2 sheets). LOCALITY NOT INDICATED: *Colenso 966, 991, 1552, s.n.* (K).

CULTIVATED: Wellington, *Gunn 226* (GH). South Island, Park Gardens, *Anderson 85* (†F), *86* (A, †Mo, NY, Ph, UC).

Podocarpus nivalis Hooker var. **erectus** Cockayne in Trans. N. Z. Inst. **48**: 199. 1916; Cheeseman, Man. N. Z. Fl. 112. 1925.

An erect shrub, 1–2 m. high. Leaves larger, sometimes nearly 2.5 cm. in length. Otherwise like the species proper. This form is found in a restricted area on South Island, but also appears in cultivation.

DISTRIBUTION: South Island, 1000 m. on Mt. Owen and Mt. Percival in Nelson Province and Cass River, Canterbury.

SPECIMENS EXAMINED:

NEW ZEALAND: South Island: Mt. Sugarloaf, Cass, *Foweraker & Cockayne 20000* (TYPE) (†A–2 sheets); Southern Alps, Canterbury, Big Ben, *Cockayne 189* (†GH); Hermitage, Mt. Cook region, *W.A. & C. B. Setchell* in 1927 (UC); ?Bay of Islands, U.S. So. Pac. Expl. Exped., *Anon. s.n.* (GH).

CULTIVATED: California, Golden Gate Park, *Eastwood* in 1916 (CAS), *Walther* in 1920 (CAS), in 1923 (A), in 1924 (A), *Walker 5165* (UC).

Podocarpus acutifolius Kirk in Trans. New Zealand Inst. **16**: 370. 1883, For. Fl. N. Z. 64. 1889; Pilger in Pflanzenreich **IV. 5**(Heft 18): 84. 1903, in Nat. Pflanzenfam. ed. 2, **13**: 247. 1926; Cockayne, Veg. N. Z. 1921, 1928; Florin in Svenska Vet.-Akad. Handl. ser. 3, 10: 279. 1931.

Podocarpus parvifolius Parlatore in DC. Prodr. **16**: 514. 1868; Dallimore & Jackson, Handb. Conif. 54. 1923, 1931, 79. 1948.

An erect-branched shrub, 1–2 m. high, branches short and rigid (in sheltered places slender), erect. Branchlets 1–1.2 mm. in diameter, green, ridged, leaf scars prominent. Terminal buds ovate, no wider than stem,

with scales lanceolate, attenuate, tip stiff and thick, base broad, with scarious erose margins. Leaves crowded (spreading and lax in sheltered places), thin, green, 1–1.5 cm., or more long, 1.5–2 mm. wide (rarely 2.5 mm.), coriaceous, narrow-linear, long-angustate, pungent; midrib prominent beneath, flat above; stomata in 2 whitish bands on underside. Pollen cones 1 or 2 (or more) fascicled on a short peduncle, each cone surrounded at base by 4 ovate acute-obtuse, broad, scarious-margined scales, 2.5 cm. long. Microsporophylls obtuse. Female cones solitary, axillary, on very short 1 mm. peduncles; receptacle of 2 or 3 fused unequal fleshy scales, the larger scale fertile, free at the obtuse tips, red. Seed narrow-ovoid, 4 mm. long, 3 mm. wide, crested.

DISTRIBUTION: Mountain districts in Marlborough, South Island. Known as the Acute-leaved Totara.

SPECIMENS EXAMINED:

NEW ZEALAND: South Island: Hope Valley, *Kirk s.n.* (A, †F, GH, †Mo); Canterbury, *Haast* in 1866 (†BR); Lake Rotoit, Nelson, *Cheeseman s.n.* (Ph.), *Anon.* ex Gordon Herb. (A); Lake Rolaiti, *Cheeseman s.n.* (K); Lake Brunner Dist., Westland, *Cockayne 6646* (A, NY); Glenhope, *Cockayne 8555* (A); Western Botanic Dist., near Waiko, *Cockayne 10022* (A–2 sheets); Omerva Saddle, *Cockayne 10020* (A); Mt. Duppa, Marlborough, *Sledge 247* (CU); Nothopip forest, Marcuia Valley, *Cockayne 13579* (K); ex Masters Herb., *Anon. s.n.* (K).

CULTIVATED: New Zealand: North Island, Ruatangata Garden, *Setchell* in 1904 (†UC, 1–2 yr. seedlings); South Island, Dunedin Botanic Garden, *Lindsey* in 1935 (CU–2 sheets). England: Kew, Royal Botanic Garden, *Cook* in 1937 (†Ill–2 sheets). United States: California, Golden Gate Park, *Eastwood* in 1916 (CAS), in 1919 (CAS), *Walther* in 1920 (†CAS), Greendale, *Anon. s.n.* (A).

Podocarpus alpinus R. Brown ex. Mirb. Geogr. Conif. in Mém. Mus. **13**: 75. 1825 (nomen!); Bennett in Horsfield Pl. Jav. Rar. 40. 1838 (nomen!); Hooker f. in Lond. Jour. Bot. **4**: 150. 1845, Fl. Tasmania **1**: 356. 1860; Endlicher, Syn. Conif. 214. 1847; Parlatore in DC. Prodr. **16**: 520. 1868; Bentham, Fl. Australia **6**: 248. 1873; Mahlert in Bot. Centralbl. **24**: 280. 1885; Kent in Veitch's Man. Conif. 148. 1900: Pilger in Pflanzenreich **IV. 5** (Heft 18): 83, f. 16E, 85. 1903, in Nat. Pflanzenfam. ed. 2, **13**: 218, f. 117E, 247. 1926; Baker & Smith, Res. Pines of Australia 442. 1910; Dallimore & Jackson. Handb. Conif. 38. 1923, 1931, 60. 1948.

Nageia alpina F. Müller in Pap. Roy. Soc. Tasmania 23. 1879.

Podocarpus alpina var. *lawrencii* Hooker f., Fl. Tasmania **1**: 356. 1860.

Podocarpus lawrencii Hooker f. in Lond. Jour. Bot. **4**: 151. 1845.

Podocarpus totara var. *alpina* Carrière, Traité Conif. ed. 2, 652. 1867.

A low shrub up to 4 m. in height, densely branched; branchlets scattered, short, spreading, thickly leafy, greenish, ridged, with leaf scars raised on pulvini. Terminal buds ovate or globose, of the same diameter as the stem;

outer scales elongate, up to 2 mm. long, keeled, erect, tip thick and broad, becoming shorter with acuminate tip; inner scales thin, keeled, broadly triangular, brown, margins scarious and erose, short apiculate, often not deciduous. Leaves spreading, coriaceous, oblong-linear, shortly rotundate or obtuse at the tip, sometimes shortly subapiculate, gradually narrowing to the sessile base, 0.5–1.2 cm. long, 1.5–2.5 mm. broad; midrib flat or slightly impressed above, broad and prominent below. Pollen cones fascicled 3–6 (solitary and sessile according to Dallimore & Jackson, 9) at the tip of peduncles 3–4 mm. long (up to 1 cm.), in the axils of short scarious-margined bracts, these sometimes as long as the leaves, decurrent on peduncle, patent, cones 6 mm. long. Microsporophylls imbricate, crowded, triangular obtuse with fairly long apiculi. Female cones on very short peduncles or sessile; receptacle small, 3 mm. long, of two fused fleshy scales with rather long free tips. Seed ovoid, 5 mm. long (or less), crested.

DISTRIBUTION: High mountain regions in New South Wales of Australia and Tasmania.

SPECIMENS EXAMINED:

AUSTRALIA: New South Wales: Mt. Kosciusko, *Maiden & Forsyth* in 1899 (A, †CAS, †Mo, UC). Tasmania: Western Mts., *Rodway* in 1929 (†A); Mt. Field, east side, *Maiden* in 1906 (†A, †BR, GH); Mt. Wellington, *Gunn 226* (†GH, YU); Sasset, Border Hill, The Warren Wood, *Jackson* in 1936 (A); *Beunit 120* (TYPE) (†BM); *O.W.F. s.n.* (†BR); *Pibrin 4* (K); ex Gay Herb., *Anon. s.n.* (GH).

CULTIVATED: England: Kew, Royal Botanic Garden, *Nicholson 68* (A), *A.R.* in 1901 (A); ex Gordon Herb. *Anon. s.n.* (A). United States: California, Golden Gate Park, *Buchholz* in 1942 (†Ill).

Podocarpus gnidioides Carrière, Traité Conif. ed. 2, 656. 1867; Pilger in Pflanzenreich **IV. 5**(Heft 18): 82. 1903, in Nat. Pflanzenfam. ed. 2, **13**: 84. 1926; Schlechter in Bot. Jahrb. **39**: 16. 1907; Guillaumin in Ann. Musée Col. Marseille ser. 2, **9**: 269. 1911, in Bull. Mus. Hist. Nat. Paris **18**: 100. 1912, Fl. France D'Outre-Mer 10. 1948; Dallimore & Jackson, Handb. Conif. 46. 1923, 1931, 70. 1948; Florin in Svenska Vet.-Akad. Handl. ser. 3, **10**: 279. 1931.

Podocarpus gnidioides var. *caespitosa* Carrière, Traité Conif. ed. 2, 656. 1867; Pilger in Pflanzenreich **IV. 5**(Heft 18): 84. 1903; Compton in Jour. Linn. Soc. **45**: 426. 1922; Dallimore & Jackson, Handb. Conif. 46. 1923, 1931, 70. 1948.

Podocarpus alpina var. *aborescens* Brongniart & Gris in Bull. Soc. Bot. France **13**: 425. 1866; Dallimore & Jackson, Handb. Conif. 46. 1923, 1931, 70. 1948.

Podocarpus alpina var. *caespitosa* Brongniart & Gris in Bull. Soc. Bot. France **13**: 425. 1866.

A small shrub 0.5–2 m. high; branches decumbent, 1.2–1.5 mm. in diameter at tip, thickly leafy, green, ridged, with prominent leaf scars, the

bark becoming greyish, the inner bark brown. Terminal bud globose, flattened, 2 mm. in diameter, outer scales oblong or narrowly triangular, keeled, with thick tips erect or scarcely spreading, becoming shorter (1 mm. long), obtuse, with incurved tips; inner scales rotundate or broadly obtuse, scarious erose margined. Leaves quite spreading, linear, rounded to obtuse at the apex, sessile, gradually narrowing at the base, shiny above, very revolute margins when dry, 1.2–2 cm. long, 1–2 mm. broad; upper midrib shallowly grooved or abruptly sulcate, sometimes quite prominent below. Pollen cones axillary, solitary on peduncle 4 mm. long, erect, cylindric, surrounded at base by broad obtuse scales with scarious margins, 1–2 mm. long. Microsporophylls crowded, scarcely apiculate. Female cones solitary, axillary on short thick peduncle 1–1.5 mm. long; receptacle of 2 fused, almost equal, fleshy scales free at the broad obtuse tips, only 3–5 mm. long, bright red at maturity. Seed ovoid, crest erect, 5–7 mm. long, 3 mm. broad.

DISTRIBUTION: New Caledonia in summit flora of mountains.

SPECIMENS EXAMINED:

NEW CALEDONIA: Mt. Dore, *Pancher 397* (P), *Pancher & Vieillard 397* (P), Pancher ex *Thoret* (K), *Pancher s.n.* (P–3 sheets), Pancher ex *Hennecart* in 1879 (K, NY), *Vieillard 3263* (P), *Virot 209* (P–4 sheets), *Buchholz 1432, 1433, 1435* (†Ill); Mt. Humboldt, *Virot 343* (†P), *Virot 422* (P), *Buchholz 1575* (†Ill), *Schlechter 15329, 15330* (†BR, K, P); Mt. Koghi, *Balansa 183* (K, NY, P–4 sheets), *Franc 2324* (A, P); Mt. Dzumac, *LeRat 154, 330* (P), *2829* (K, P–2 sheets, *Franc 532* (A, †BM, †LA, NY, P, †UC); Mt. Mou, *M. de Pompéry* in 1880 (P); Montagne des Sources, *MacDaniels s.n.* (†CU); Bourare, *Cribbs 1183* (†P); Ile de Pins, *Jeanneney s.n.* (P). LOCALITY NOT INDICATED: *Muller 70* (type coll., †P–2 sheets), *Muller s.n.* (P).

CULTIVATED: United States, California, *Buchholz* in 1942 (Ill).

Orr discusses *Podocarpus gnidioides* as a New Caledonian plant among the species in his geographical area (b) Asiatic, Malayan and Polynesian, but he emphasizes its relationship to the New Zealand species. He described the hypodermal fibers as "frequently superimposed on one another" and neatly packed together to "produce a characteristic mosaic appearance." This is very striking and, on examination of transverse leaf sections, easily differentiates this species from the others in subsection D.

In 1866 Brongniart and Gris (1) described a tree which they called *Podocarpus alpina* var. *arborescens* from a *Muller* specimen collected in 1862. At the same time they described the shrub from Mt. Dore, New Caledonia, and named it *P. alpina* var. *caespitosus*. In the Paris Museum there now exist two similar *Muller* specimens, both *#70*. The herbarium labels of these give both Australia and New Caledonia as collection regions and one describes the plant as a "taxad" tree, 40 ft. high, with the habit of a *Sequoia*. It is a sterile specimen and a tag on it says "like *Taxus* New Cal." The other *#70* does not indicate habit. After almost a century, in which many collectors, notably Pancher and Vieillard, and in recent years Compton, Buchholz, Chevalier and others have made extensive

collections on New Caledonia, such a tree has not been seen again. I have examined the leaf anatomy of the first of the *Muller* specimens and do not observe any difference from that found in a large number of shrubby specimens from different mountain regions in New Caledonia. It is always characteristic. Compton (7) indicated that he could not find any difference in the external appearance of the foliage. It is now doubtful if it ever existed as a tree and it is probable that there was some confusion at the time labels were attached to the specimens.

Carrière (4) recognized the tree and the shrub as a distinct species from *Podocarpus alpinus*, naming them *P. gnidioides* with a variety *caespitosus*. Unfortunately he selected the now doubtful tree for the type and made the shrub the variety. The life history of the shrub is completely known. Since the tree habit is the only vegetative difference, buds, twigs, and leaves all being the same, it now seems most desirable to omit from the description the existence of a tree except as a mere possibility. Prof. Buchholz, when pursuing his extensive studies of New Caledonian conifers, reached the decision to drop the use of the variety *caespitosus*. This is consistent with the rules of nomenclature in that *Muller #70* is obviously the type of *P. gnidioides* and it is identical with the plant we now know.

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PHLOEM POLARITY IN BARK REGENERATION [1]

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THE POLARITY of phloem transport is the basis for checking tree growth by inverting a ring of bark on the trunk of the tree (7). If a ring of bark is removed, turned upside down and held firmly against the xylem with a rubber band, it will reunite with the wood. The inverted ring of bark will continue to form xylem, but the growth is slow, due to the checking of phloem transport by the reversed polarity. The bark formed at the vertical seam of the inverted ring does, however, make normal growth, presumably due to its normal polarity. As a result the dwarfing effect of the inverted ring of bark is temporary, because normal phloem transport is soon established in the bark regenerated at the vertical seam.

In order to test the origin of the regenerated bark at the vertical seam of a ring of bark grafted on a woody stem we grafted a ring of bark from an apple tree with red wood and bark onto an apple tree with white wood and green bark. In the first experiment the ring of red bark was grafted in the normal position in early June. By the end of the growing season it was evident that the new wood formed beneath the ring of red bark was red, but that the wood formed at the vertical seam was white. Obviously the new wood and bark was derived from the regeneration of the underlying xylem elements rather than from the adjacent bark. The growth of xylem was essentially the same whether derived from the regenerated bark or from the ring of red bark, as is shown in FIGURE 1.

In the second experiment a ring of red bark was grafted, upside down, on a branch with white wood. The xylem formed under the red bark was red, but there was comparatively little wood formation under the ring of red bark as is shown in FIGURE 2. The wood formed at the vertical seam was white and made essentially normal growth. It is evident that the cambium regenerated at the vertical seam is derived from the underlying wood and not from the cambium of the adjacent bark. It is also evident that the growth of the xylem at the vertical seam is normal, regardless of the orientation of the adjacent bark. The growth of the xylem beneath the inverted ring of bark is, however, greatly suppressed, presumably because of the reversed polarity of the phloem.

The polarity of phloem regenerated from the surface of the xylem does not appear to be determined by the orientation of the adjacent cambium yet the adjacent cambium seems to play a role in the formation of new cambium. In *Hibiscus*, according to Sharples and Gunnery, the exposed wood, following removal of the bark, produces large thin walled cells derived from the ends of the medullary rays and smaller cells from meristematic cells which are normally destined to form xylem. If kept moist these cells form a parenchymatous cushion about a millimeter deep in two or

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three weeks. New cambium is then formed across the callus cushion, beginning where the callus is in contact with the cambium of the adjacent bark and "like a slowly closing diaphragm sweeps gradually inward until opposing edges meet. . ." (8). The cambium then produces new wood and bark.

According to Sharples and Gunnery both bark callus and wood callus are formed largely from medullary ray elements. Since the medullary rays are oriented across the long axis of the stem and pass from the xylem through the cambium to the phloem they would not be expected to be polarized in a vertical direction. How then does the phloem derived largely from medullary ray elements become normally polarized? Sharples and Gunnery observed that "new cambial elements do not appear except in close proximity to pre-existing cambial elements" yet the polarity of the resulting phloem cells do not appear to be influenced by the adjacent inverted cambium.

In order to further test the effect of adjacent cambial tissue on the orientation of regenerated phloem and xylem an experiment was designed based upon a technique described by Garner (1). Squares of bark a little more than an inch in diameter were removed from young apple trees with white wood, and replaced with squares of bark from apple trees with red wood. A smaller square of bark about a third of an inch in diameter was removed from the center of each of the red squares leaving the white wood exposed, surrounded on all sides by red bark. The grafts were covered with polyethylene film to keep the exposed wood moist, and the grafted bark was bound firmly with a rubber band until it was united with the wood.

The blocks of red bark were oriented in the normal position, upside down and laterally on the white wood. At the end of the growing season the grafts were removed and sectioned. As shown in FIGURE 3 the normally oriented graft made much more growth, both of the wood beneath the red bark and that from the regenerated cambium, than those in the inverted (FIG. 4) or transverse (FIG. 5) position. In all cases, however, the regenerated xylem was oriented in a vertical position, regardless of the orientation of the grafted square of red bark (FIG. 6). It is evident that the orientation of the cambium regenerated from the white wood is not determined by the orientation of the adjacent cambium.

When the grafted bark is oriented in a normal position there is only a slight overgrowth of the normal tissue above the graft and a comparatively uniform growth of the grafted bark along its entire length as is shown in FIGURE 3. Such a uniform growth would be expected if normal phloem transport in the graft were soon established. However, when the grafted bark is oriented in an inverted or transverse position, there is considerable swelling of the normal tissue above the graft and differential growth in the grafted bark as is shown in FIGURES 4 and 5. The swelling above these grafts can be attributed to the blocking of normal phloem transport and the resulting accumulation of nutrients and hormones above the graft. The differential growth within the length of the graft can be attributed to the diffusion of nutrients and hormones accumulated above the graft. The diffusion must be slow because the growth of the inverted or transverse graft

is greatly reduced, but the greater growth at the upper end of the grafted bark indicates that some nutrients are diffused into this tissue. This greater growth at the upper junction of the graft (A, FIGS. 4 and 5) can not be attributed to growth stimulation by "wound hormones," because no such differential growth is found at the lower end of the graft union, either at the union between the abnormally oriented bark and the upper end of the regenerated bark (B, FIGS. 4 and 5), or between the transverse or inverted bark and the lower union with the normal bark (D). There is, however, a secondary swelling at the junction of the lower end of the regenerated bark and the abnormally oriented bark (C). Apparently the diffusion of nutrients continues down the inverted or transverse bark to some extent and the nutrient sap passes freely into the regenerated bark, since the regenerated bark is normally polarized. But when it reaches the base of the regenerated bark it must then pass by diffusion into the inverted or transverse grafted bark and tends to accumulate and promote increased growth at the upper end of the abnormally oriented bark. The growth in this region is much less than at the upper junction of the graft because the nutrients have been greatly diminished by blocking of phloem transport in the upper part of the graft.

The inversion of a ring of bark on the trunk of the tree suppresses growth by checking phloem transport down the trunk of the tree and thus decreasing the flow of organic nutrients to the roots. The effect of the bark inversion is temporary, however, due to the regeneration of normally polarized phloem and xylem. If a single ring inversion is made, the normally polarized elements regenerated at the vertical seam grow so rapidly that the dwarfing effect of the inverted ring of bark is soon lost, especially in young vigorous trees. We have attempted to avoid this restoration of normal phloem transport by using two inversions with the vertical seams on the opposite side of the trunk of the tree. Restoration of normal transport is delayed, but not prevented, by this technique.

When a second inverted ring of bark is grafted directly above the first one, the growth of the tree is checked for several year. The descending sap moves down the phloem regenerated at the first vertical seam, but is checked by the second inverted ring of bark. There is, however, a lateral movement of the nutrient sap, particularly in the lower inverted ring of bark, so that eventually it makes contact with the regenerated phloem of the lower vertical seam on the opposite side of the trunk of the tree. This lateral diffusion of sap is followed by a lateral orientation of the new phloem and xylem. Eventually normal phloem transport is established down the regenerated phloem at the first vertical seam and then laterally across the lower end of the upper inversion, and the upper end of the lower inversion, to the regenerated phloem at the second vertical seam and then on down the stem.

When the two inversions are made with a ring of normal bark between them the nutrient sap descends the regenerated phloem at the vertical seam of the first inversion, but can pass by lateral diffusion across the ring of normal bark to the upper end of the regenerated phloem of the seam of the second inversion. The xylem and phloem of the normal ring of bark

soon become oriented transversly at a downward angle to establish a continuity of normal phloem transport. Such a double bark inversion was made on a young poplar tree in June. At the end of the growing season the bark was removed to show how the xylem had grown at the vertical seams on opposite sides of the trunk and were connected by reoriented xylem

DESCRIPTION OF FIGURES

FIGURE 1. Cross section of an apple branch with white wood on which was grafted, in June, a ring of bark from an apple tree with red wood. At the end of the growing season the sectioned stem showed that the red bark had produced a normal growth of red wood beneath it. The wood produced at the vertical seam was white, proving that this bark and wood was regenerated from the surface of the white wood and not from the adjacent red bark.

FIGURE 2. Cross section of a ring of red bark grafted in an inverted position on an apple stem with white wood. At the end of the growing season the inverted ring of bark had produced little red wood, due to the reversed polarity of the phloem. The regenerated white wood made normal growth, indicating that the phloem regenerated from the white wood was normally polarized.

FIGURE 3. Longitudinal sections of an apple stem with white wood on which had been grafted a square of red bark after removing a small square of bark from the center of the red bark. The wood developed under the red bark was red and that regenerated from the exposed white wood in the center was white. When the red bark is grafted in the normal position the growth of the underlying red wood and of the regenerated white wood in the center is essentially normal.

FIGURE 4. Same as above, but red bark inverted. The growth of the wood, both under the red bark and under the regenerated bark is greatly reduced, due to blocking of phloem transport by the reversed polarity of the phloem of the grafted red bark. There is evidence of diffusion of nutrient sap into the grafted tissue as indicated by greater growth of wood at the upper end of the graft.

FIGURE 5. Same as above, but with grafted bark oriented in a transverse position.

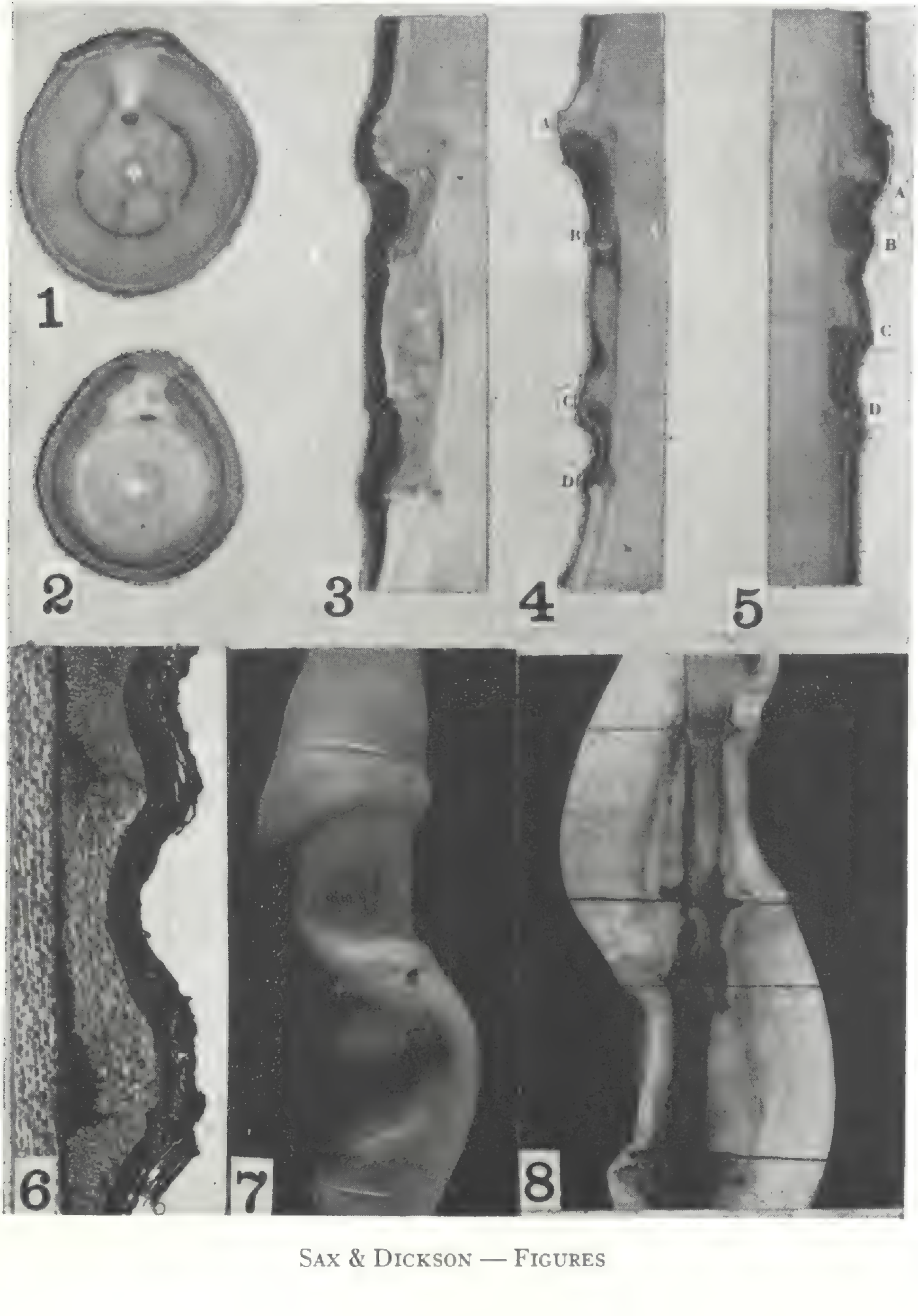
FIGURE 6. An enlarged section of the graft shown in FIG. 5. The red xylem is oriented transversely, but the xylem produced by the cambium from the tissue regenerated from the exposed white wood is normally oriented.

FIGURE 7. Orientation of xylem of a poplar stem at end of growing season after making a double bark inversion in June. The two bark inversions, with their vertical seams on opposite sides of the stem, were separated by a ring of normal bark. The regenerated bark at the vertical seam was normally polarized, permitting normal phloem transport. The nutrient sap descended the phloem of the upper regenerated bark at the seam, diffused laterally across the ring of normal bark and down the normally polarized seam of the lower inverted ring of bark. The lateral diffusion of the sap across the normal ring of bark was followed by a reorientation of phloem and xylem, establishing normal phloem transport and normal xylem growth by the end of the season.

FIGURE 8. Longitudinal section of a poplar stem following a double bark inversion as described for FIG. 7. Note greatly restricted growth of xylem beneath the inverted rings of bark, due to reversed phloem polarity.

across the stem under the normal ring of bark between the two inversions (FIG. 7). A longitudinal section of a poplar stem subjected to the same type of double bark inversion is shown in FIGURE 8.

The regeneration of new bark from exposed wood and the reorientation of the xylem and phloem has long been known. Thomas Andrew Knight in 1807 (3) referred to the work of Henri Louis Duhamel done more than



SAX & DICKSON — FIGURES

fifty years earlier. If a piece of bark is removed from a tree and the exposed wood is kept moist, "a glareous fluid exudes from the surface of the alburnum; this fluid appears to change into a pulpous mass, which subsequently becomes organized into cellular matter. . .". A more modern and detailed description of this process was described by Sharples and Gunnery in 1933 (8).

Knight was also aware of the origin of new wood formed beneath a strip of grafted bark. In 1808 he wrote as follows: "Having procured, by grafting, several trees of a variety of apple and crab tree, the woods of which are distinguishable from each other by their colours, I took off, early in the spring, portions of bark of equal length, from branches of equal size, and I transposed these pieces of bark, inclosing a part of the stem of the apple with a covering of bark from the crab tree, which extended quite around it and applying the bark of the apple tree to the stem of the crab in the same manner. . . . A vital union soon took place between the transposed pieces of bark and the alburnum . . . and in the autumn it appeared evident that a layer of alburnum had been, in every instance, formed beneath the transposed pieces of bark." (4).

The reorientation of newly generated xylem and phloem was also observed by Knight (3). He found that the new vessels "may be made, by appropriate management, to traverse the new cellular substance in almost any direction," by controlling the direction of flow of the nutrient sap. In 1862 Hartig (2) described the reorientation of the xylem in the new wood developed above a spiral deletion of a strip of bark. These and other experiments, which show that the direction of flow of the nutrient sap controls the orientation of the newly formed xylem and phloem, have been described more recently, and in more detail, by MacDaniels and Curtis (6). The vessels gradually become reoriented so that they are parallel with the spiral.

SUMMARY

The inversion of a ring of bark on the trunk of a tree results in checking phloem transport to the roots and dwarfing the tree. The effect is not permanent because the new bark regenerated at the vertical seam is normally polarized and permits normal phloem transport. By grafting a ring of bark from an apple tree with red wood on a tree with white wood, it has been shown that the new bark and wood regenerated at the vertical seam of the grafted ring of bark is derived from the underlying wood and not from the adjacent bark.

A double bark inversion, with the vertical seams on the opposite sides of the trunk, increases the duration of the dwarfing effect, but the lateral diffusion of nutrient sap soon results in a lateral orientation of the new xylem and phloem, to bridge the normally polarized tissues regenerated at the seams of the two inverted rings of bark.

The nutrient sap may diffuse laterally or vertically if normal phloem transport is checked.

If a strip of bark is removed from a tree, the exposed wood, if kept moist, will regenerate new bark and wood. It is shown that the new cambium is oriented in the long axis of the stem, regardless of the orientation of the surrounding grafted bark.

The general conception of the regeneration of new growth from exposed wood, and the control of the orientation of xylem and phloem by the direction of flow of nutrients, dates back to the work of Knight early in the 19th century. These ideas, supplemented by more detailed analyses in later years, are of value in designing experiments dealing with the practical problems of controlling tree growth.

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NEW SPECIES IN THE BAMBOO GENUS PHYLLOSTACHYS AND SOME NOMENCLATURAL NOTES

F. A. McCLURE [1]

IN 1945 eight new species of the genus *Phyllostachys* were described [2] from the collection of living plants maintained by the U. S. Department of Agriculture at one of its field stations, the Barbour Lathrop Plant Introduction Garden, near Savannah, Georgia. Since that time, among the phyllostachid bamboos growing there, four additional species presumed to be new to science have advanced sufficiently in their development toward maturity to show characteristics of a distinctive nature. The following Latin descriptions [3] were prepared on the basis of living plants growing under the respective U. S. D. A. Plant Introduction numbers cited. Type specimens are deposited in the U. S. National Herbarium, duplicates in the herbarium of the National Arboretum.

Phyllostachys bissetii McClure sp. nov. FIG. 1.

Culmi usque ad 6.75 m. alti et 25 mm. diametro; *internodia* viridia usque ad 33 cm. longa (in culmo 6.75 m. alto, ut exemplo electo, internodio duodecimo maximo longitudine) omnia glabra vel inferiora saepius sursum setis erectis brevissimis parce sparsa, delapsis tegentibus vaginis laxe pruinosa; *nodi* pulvino cicatriceque modice et subaequaliter eminentes, cicatrice glabra. *Culmi vaginae* ad apicem truncatum sensim rotundatae vel angustatae, dorso glabrae (inferiores tantum primo interdum dorso pubescentes marginibus ciliatae) virides saepe vino passim tinctae haud maculatae; *auriculae* plus minusve valde evolutae (ambae alterutra interdum obsoletae) ovatae vel oblongae vel late falcatae margine *setis* rigidis scabris radiatim dispositis munitae; *ligula* brevis vino tincta, apice leviter convexa, margine plus minusve asymmetrica, setis hispido-albidis fimbriata; *vaginarum laminae* infimae anguste subtriangulae superiores gradatim usque ad formam lineari-lanceolatum mutantes, apice naviculiformes, inferiores appressae vel raro valde reflexae, superiores plus minusve patentes. *Foliorum vaginae* nonnullae auriculatae; *auriculae* margine setis radiatim fimbriatae; *ligula* modice evoluta; *foliorum laminae* lanceolatae vel oblongo-lanceolatae, subtus sparsim et invalide scabrae. *Inflorescentiae* desunt.

[1] Plant Introduction Section, Horticultural Crops Research Branch, Agricultural Research Service, U. S. Department of Agriculture.

[2] McClure, F. A. The vegetative characters of the bamboo genus Phyllostachys and descriptions of eight new species introduced from China. Wash. Acad. Sci. J. **35**: 276–293. 1945. (Sept. 15).

[3] A field manual under preparation will provide English descriptions and a field key for the identification of all of the bamboos of this genus known to be under cultivation in the Western Hemisphere.

Type in U. S. National Herbarium, Nos. 2177861–2 (2 sheets), collected by *F. A. McClure* (No. 21801), April 22, 1955 at the U. S. Barbour Lathrop Plant Introduction Garden where the plant is cultivated under P. I. 143540. The description is based on the living plants in a colony about 13 years old. Propagating material of this bamboo, from plants under cultivation at Chengtu, Szechwan province, China, was secured by John Tee-Van and brought to this country late in 1941 for the Plant Introduction Section of the U. S. Department of Agriculture.

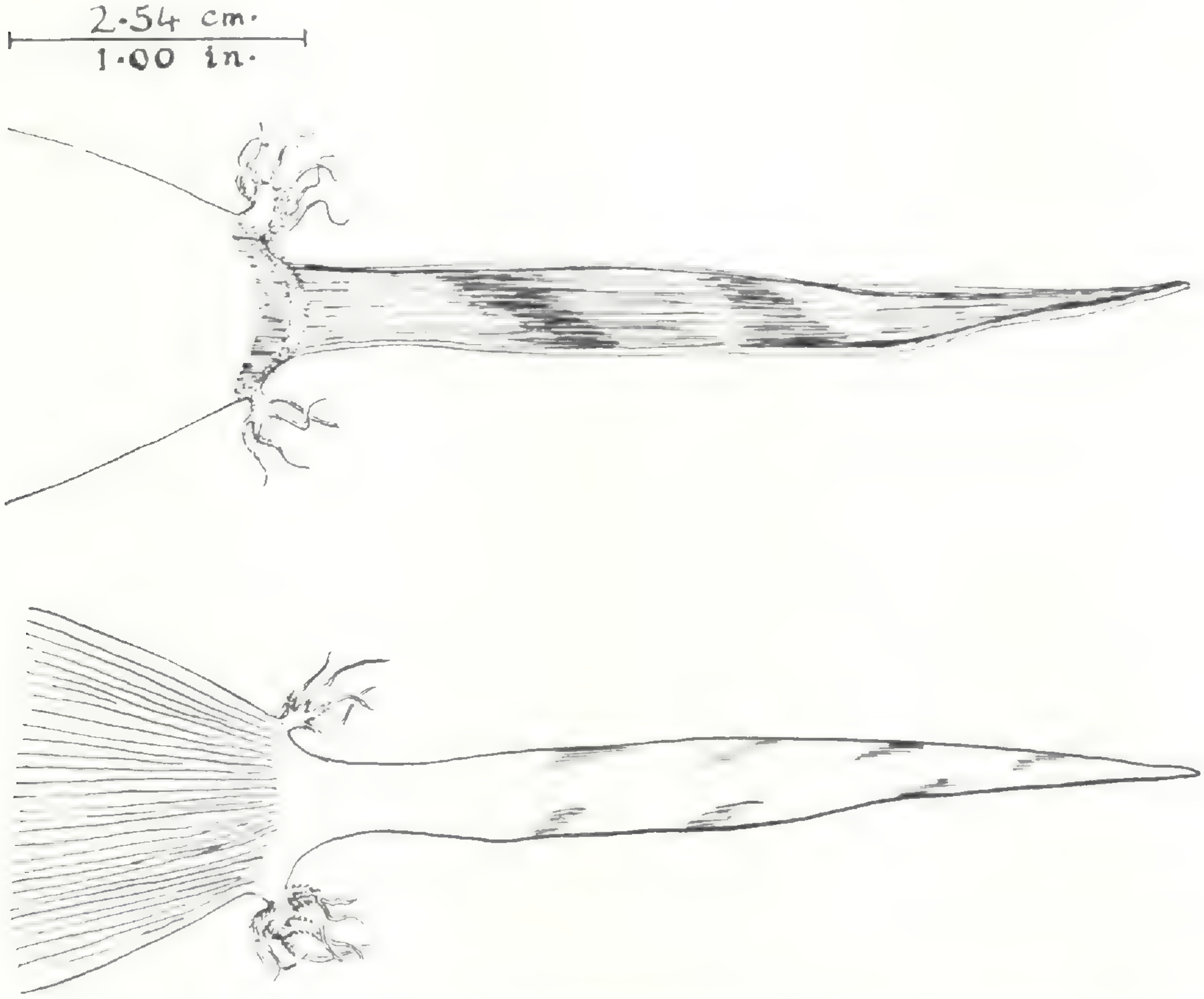

FIG. 1. *Phyllostachys bissetii* McClure sp. nov. Inner (above) and outer aspects of the apex of a mid-culm sheath.

The specific epithet signalizes the outstanding contribution to the development of popular interest in bamboo culture and utilization made by David Bisset as Superintendent of the U. S. Barbour Lathrop Plant Introduction Garden.

Phyllostachys bissetii is in some respects rather similar to *Ph. aureosulcata*, from which it is distinguished by the very sparse instead of dense pubescence of the lower internodes of the culms, by its lack of sharply defined color-striping in the culm sheaths, and by minor differences in the shape of the apical structure of the culm sheaths. Moreover it lacks the yellow color-panel on the groove, a stable feature characteristic of the

internodes of young culms of *Ph. aureosulcata*. *Phyllostachys bissetii* is one of the first to initiate the growth of new shoots in spring. According to Mr. Bisset, it has shown signs of being one of the hardiest of the phyllostachids under observation at the Barbour Lathrop Garden.

In 1941, during the course of the New York Zoological Society's expedition to Australia and China, of which he was the leader, Mr. Tee-Van received two young Giant Pandas as a gift from the Chinese people to the American people. During their long voyage across the Pacific, these animals were fed with leafy branches of this bamboo and several other kinds. However, the bamboo on which the Giant Panda is known to feed *in its native habitat* is another species, a member of the genus *Sinarundinaria*. Unfortunately plants of the latter species introduced by Mr. Tee-Van at the same time did not survive.

Phyllostachys decora McClure sp. nov. FIG. 2.

Culmi usque et ultra 7 m. alti et 30 mm. diametro, virides, delapsis tegentibus vaginis nodis et internodiis sursum primiter setis perbrevibus retrorsis sparsim scabris deinde sensim glabrescentibus, primo haud vel

FIG. 2. *Phyllostachys decora* McClure sp. nov. Inner (below) and outer aspects of apex of a mid-culm sheath.

leviter glaucescentibus deinde sub nodos dense pruinosi; *internodia* interdum leviter striata, usque ad 15.8 cm. longa (in culmo 7.2 m. alto, ut exemplo electo, internodio undecimo maximo longitudine); *nodi* pulvino cicatriceque modice et subaequaliter eminentes, cicatrice glabra. *Culmi vaginae* ad apicem latum truncatumque subito rotundatae dorso glabrae haud pruinosae, immaculatae vel maculis minutis fuscis sparsim maculatae,

et porro colore saturato-viridi, viridi pallidiori alboque in longitudinem variegatae, interdum omnino paene albae, secundum margine purpura notatae; *auriculae* 1 vel 2 vel nullae, variabiles, angustatae falcatae fuscae nudae vel setis paucis invalidis fuscis margine fimbriatae; *ligula* primiter purpurata latissima et comparate brevis, apice truncata vel leviter undulata vel invalide convexa margine ciliis albis et setis crassis scabris fuscis fimbriata; *vaginarum laminae* late lanceolatae usque ad liguliformes, apice subito acutae, infimae appressae superiores appressae vel plus minusve patentes interdum invalide undulatae. *Foliorum vaginae* invalide auriculatae, *auriculis* plerisque parvis saepe obsoletis; *setae orales* paucae fragiles et fugaces; ligula vix exserta primiter purpurata; *foliorum laminae* subtus invalide et sparsim scabrae.

Type in U. S. National Herbarium, Nos. 2177856–8 (3 sheets), collected by *F. A. McClure* (No. 21757), April 16, 1953, from a colony cultivated under P. I. 128789 at the U. S. Barbour Lathrop Plant Introduction Garden. The description is based on the living plants in a colony about 15 years old.

Plants of this bamboo from the Hoi Wai Monastery, Lung Chi Mt., near I-Ming, Kiangsu province, China, where it is known by the Chinese (National) vernacular name *Mei Chu* (Beautiful Bamboo), were sent by the writer to the U. S. Department of Agriculture in 1938.

This species is readily distinguished from all the others of which the vegetative characteristics are known by the broad, truncate apex of the culm sheath and the broad but short purple ligule exserted on each side of the strap-shaped sheath blade.

Phyllostachys elegans McClure sp. nov. FIG. 3

Culmi usque paene ad 10 m. alto et 54 mm. diametro, omnino glabri; *internodia* viridia inferiora comparate brevia, superiora usque et ultra 30 cm. longa (in culmo 9.88 m. alto, ut exemplo electo, internodio vicesimo primo maximo longitudine) graciliter striata, primiter laxe et copiose pruinosa; *nodi* pulvino colorato et cicatrice glabra modice et subaequaliter eminentes. *Culmi vaginae* versus apicem angustum sensim angustatae, dorso glabrae vel interdum in lateribus scabrae vel sparsim setosae, marginibus glabrae vel subtiliter ciliolatae, primiter omnino manifeste pruinosae, dilute luteo-virides, secundum nervos purpura laeviter tinctae et porro maculis parvis fuscis discretis vel in lineis directis junctis dorso omnino notatae; *auriculae* ambae alterutra nunc defectae nunc valde evolutae, falcatae, apicem tantum secundum marginem crebre dispositis *setis* longis curvis munitae; *ligula* apice convexiuscula, comparate angusta, ca. 2 mm. alta demptis setis marginalibus, margine undulato setis pallidis crassis subglabris fimbriata; *vaginarum laminae angustae* liguliformes canaliculatae apice attenuatae pleraeque valde crispae et reflexae. *Foliorum vaginae* vulgo auriculatae; *auriculae* margine *setis oralibus* munitae; *ligula* exserta vulgo purpurata; *foliorum laminae* late lanceolatae basi rotundatae

apice abrupte acuminatae, vulgo 100 × 17 mm. interdum usque ad 180 × 22 mm., subtus ubique dense puberulae.

Type in U. S. National Herbarium, Nos. 2177863–4 (2 sheets) collected by *F. A. McClure* (No. 21802), April 24, 1955, from the colony cultivated under P. I. 128778 at the U. S. Barbour Lathrop Plant Introduction Garden. The description is based on the living plants in a colony about 15 years old.

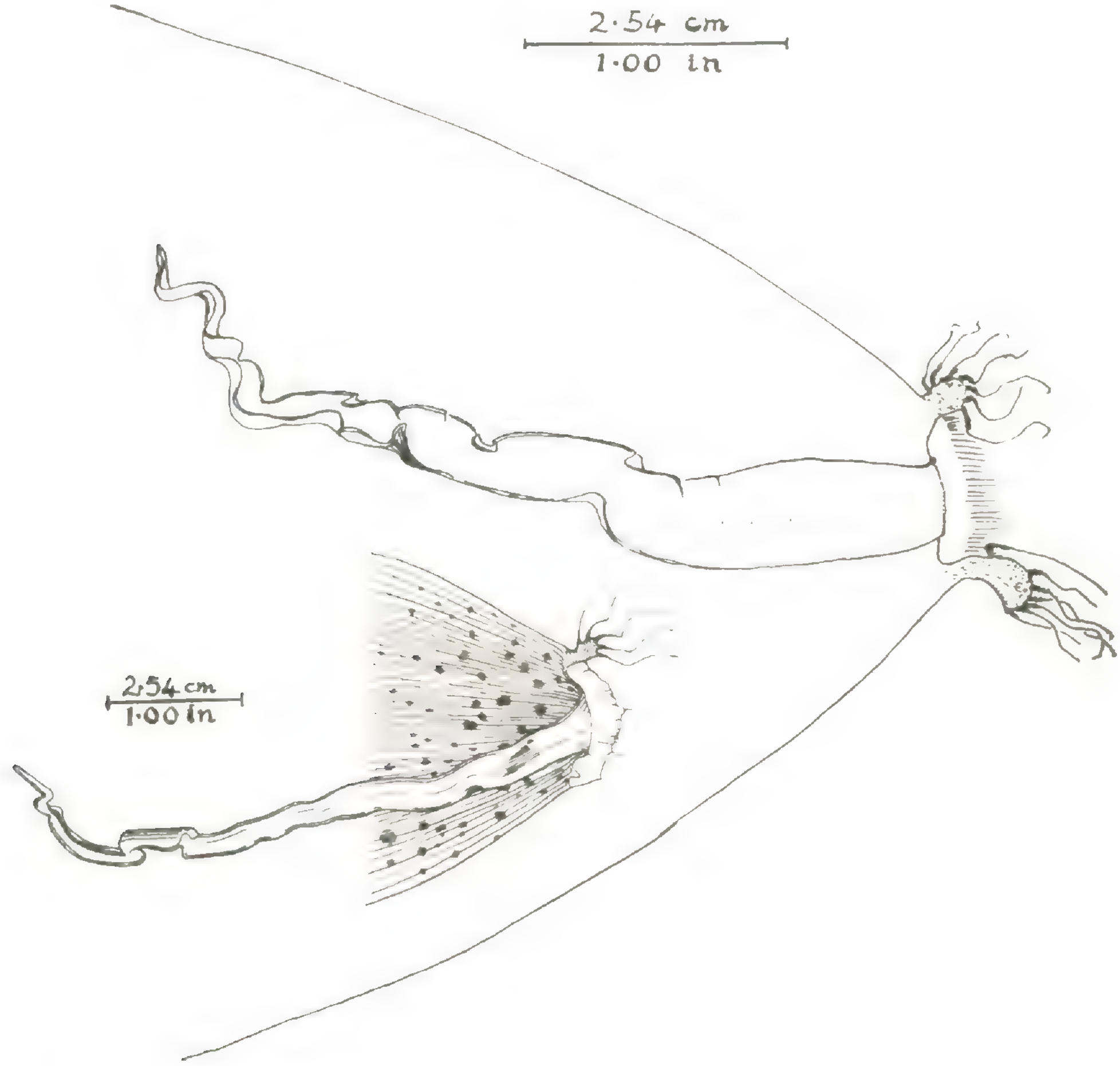

FIG. 3. *Phyllostachys elegans* McClure sp. nov. Outer aspect of apex of a mid-culm sheath: above, intact specimen; below, specimen showing but one well-developed auricle and a ligule from which most of the marginal bristles have been lost.

The type colony of this bamboo was developed from propagating material secured at Ta Ts'it, near Hung Mo Mt., Tan District, Hainan Island, China, sent by the writer to the U. S. Department of Agriculture in 1938. The local Chinese (Cantonese) name *Fa Chuk* (Flowered or Embroidered Bamboo) alludes to the conspicuous maculation of the culm sheaths. An earlier introduction, representing what appears to be a somewhat less vigorous strain of the species, is P. I. 110511, secured by the

writer at Mung Haang, Ts'ing-yuen District, Kwangtung province, China, and sent to the U. S. Department of Agriculture in 1936.

This species resembles *Ph. viridi-glaucescens* A. & C. Riv. in the appearance and variability of its culm sheaths; those of *Ph. elegans*, however, show a distinctly shorter ligule. Plants of these two species show little similarity in general appearance and *Ph. elegans* may be distinguished readily in the field by the more strongly tapered culms, the marked striation of the internode surface, and the visibly shorter internodes in the lower part of the culms. The leaf blades of the new species are smaller (shorter but proportionately broader) than those of *Ph. viridi-glaucescens*, and, in contrast with the latter, distinctly puberulent throughout the lower surface. The Chinese (Cantonese) vernacular name used in Mung Haang — *Man Sun* or *Man Chuk* (Elegant Shoot or Elegant Bamboo) — is the basis of the specific epithet.

Phyllostachys glauca McClure sp. nov. FIG. 4

Culmi usque et ultra 10 m. alti et 4 cm. diametro; *internodia* viridia, omnino glabra, delapsis tegentibus vaginis primo pulvere albo pulchre pruinosa, haud striata, usque et ultra 40 cm. longa (in culmo 10.22 m. alto, ut exemplo electo, internodio quarto decimo maximo longitudine) recta vel rarissime supra basin nonnulla leviter anfracta; *nodi* pulvino cicatriceque modice et subaequaliter eminentes, cicatrice glabra. *Culmi vaginae* ad apicem angustum truncatum sensim rotundatae vel angustatae dorso glabrae, ubique virides cum vino plus minusve valde suffusae, maculis fuscis (praesertim in basi apiceque) parce maculatae, raro paene immaculatae; *auriculae setae oralesque* raro evolutae; *ligula* fusca, lata et comparate brevis, apice truncata vel leviter undulata, raro (infimae tantum) concava, margine ciliata raro (praesertim superiores) invalide fimbriata; *vaginarum laminae* lanceolatae usque ad lineari-lanceolatae in apice hebete acuto subito angustatae, planae vel leviter naviculiformes, inferiores reflexae superiores patentes. *Foliorum vaginae* plerumque haud auriculatae; *ligula* valde evoluta primo saepius leviter purpureo-tincta; *foliorum laminae* subtus primiter secundum costam parce pilosae alibi subglabrae vel glabrescentes. *Inflorescentia* desunt.

Type in U. S. National Herbarium, Nos. 2177865–6 (2 sheets), collected by *F. A. McClure* (No. 21803), April 24, 1955 at the U. S. Barbour Lathrop Plant Introduction Garden where the plant is cultivated under P. I. 77011. The description is based on the plants in a colony about 27 years old.

Rhizomes of this species, from a garden in Nanking, Kiangsi province, China, were sent to the U. S. Department of Agriculture by the writer in 1926. They gave rise to rooted plants that survived quarantine and ultimately became established as P. I. 77011 at the U. S. Barbour Lathrop Plant Introduction Garden.

The specific epithet alludes to the distinctive misty green color of the young culms which is due to their evenly distributed overall covering of white powder. By this character this bamboo can readily be recognized in the field, even at a considerable distance.

This species is very similar to *Ph. flexuosa* in many respects. The ligules of the culm sheaths in *Ph. glauca* are broader and shorter in proportion, and fringed on the margin with minute cilia rather than bristles; they are somewhat more durable (less fragile) on drying. The blades of the culm

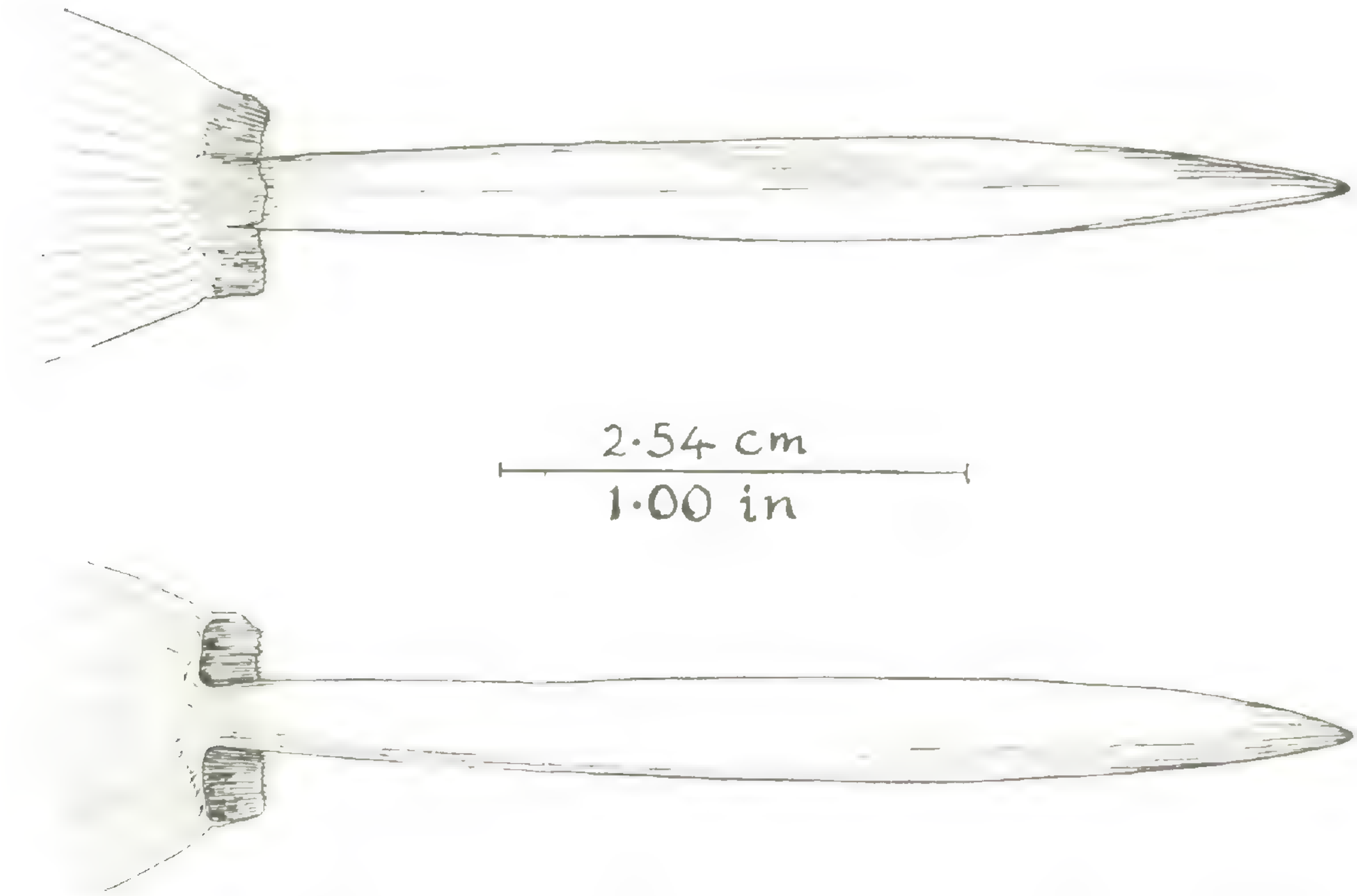

FIG. 4. *Phyllostachys glauca* McClure sp. nov. Inner (above) and outer aspects of a mid-culm sheath.

sheaths (particularly in the lower half of the culm) are appreciably broader in proportion to their length, and more abruptly narrowed at the tip than those of *Ph. flexuosa*. The culm sheaths in *Ph. glauca* are appreciably thicker and tougher in texture, and generally show fewer and more discrete dark spots than those of *Ph. flexuosa*. Plants of *Ph. glauca* (P. I. 77011) show greater vigor and larger ultimate stature than those of *Ph. flexuosa* (P. I. 52686 and 116965) under apparently identical growing conditions.

NOMENCLATURAL NOTES

Because of faulty original documentation, several of the names currently used for entities in the genus *Phyllostachys* are in need of critical examination. Among these are the following:

Phyllostachys edulis (Carr.) H. de Leh. (Houzeau de Lehaie is referred to hereinafter also as Houzeau). See discussion under *Ph. pubescens*.

Phyllostachys mitis A. & C. Riv. See discussion under *Ph. viridis*.

Phyllostachys reticulata (Rupr.) C. Koch. See discussion under *Ph. bambusoides.*

Phyllostachys sulphurea var. *viridis* R. A. Young. See discussion under *Ph. viridis.*

Phyllostachys bambusoides S. & Z., K. Bayer. Akad. Wiss. Abh. 3: 746, *pl. 5, fig. 3.* 1843. (Type species of the genus; based on a flowering specimen)

? *Bambusa reticulata* Rupr., St. Petersb. Acad. Mem. VI Sci. Nat. 3: 148. 1839. (Based on a sterile leafy specimen); *Phyllostachys reticulata* (Rupr.) C. Koch., Dendr. 2(2): 356. 1873.

Madake of Japanese gardens.

From available evidence there appear to be grounds for reasonable doubt that Ruprecht's species is the same as *Phyllostachys bambusoides* S. & Z., the Chinese bamboo known universally in Japanese gardens as *Madake.* If the problem involved only the matter of priority, *Ph. reticulata* (Rupr.) C. Koch would clearly be the correct name for this bamboo. However, the identity of the type of *Bambusa reticulata* Rupr., which is the basis of *Ph. reticulata*, has not been clearly established. So the taxonomist is still confronted with the question, is it the *Madake* of Japanese gardens, or is it something else?

Let us consider the evidence, beginning with Ruprecht's description and notes (loc. cit.)

"59. B. reticulata n. sp. Culmi ramulis foliiferis *dense* fasciculatis, laevigatis, nitidis, nodis biannulatis parum tumentibus; vaginis inferioribus aphyllis, superioribus foliolo brevissimo sub 2 lineali appendiculatis, supremis 4–5 foliiferis, omnibus striato-sulcatis, *vix* compressis, glabris, margine subciliatis, ore *fimbriatis*, fimbriis mox evanescentibus; foliis lineari-lanceolatis (6–8: 48–70) acuminatis, basi in petiolum longiusculum (sub 2 lin.) attenuatis, firmis, pergamenis, glaberrimis, supra striatis, *subplicatis*, subtus glaucescenti-cinereis.

V. sp. japonica (veros. c. Nangasaki lecta): Langsdorf!

"Ad ramulos (juniores ?) nunc descriptos haud cum dubio pertinent folia, omnibus proprietatibus descriptis similia, sed omni dimensione *majora*, pedalia et ultra, 2–3 poll. *lata*, inferiora magis ovata, latiora, superiora lanceolata, petiolo 6 lin. ad insertionem articulato, tumido, 2 lin. lato; lamina basi inaequalitera, secus costam mediam subtus valde prominulam ad latus magis evolutum, imprimis basi breve puberulo-tomentosa; nervis in q.l. 14 primariis, secundariis 9–11 venulis transversis (ut supra) creberrimis, anastomosantibus, inde parenchyma in *quadrotula minima* supra et subtus dispartientibus. (B. reticulata.)"

The last paragraph of the description, a very long one consisting of numerous references and many quotations from existing literature, has been omitted here for economy of space, since it sheds no light on the question under consideration.

Let us first direct our attention to the formal description (the first paragraph) ostensibly based on Langsdorf's specimen cited immediately

thereafter. "Culmi ramulis foliiferis *dense* fasciculatis" describes a character not found in any known species of *Phyllostachys*. Again, the statement "vaginis inferioribus aphyllis, superioribus foliolo brevissimo sub 2 lineali appendiculatis, supremis 4–5 foliiferis" is based on a condition that would not be found in any known species of *Phyllostachys* since in this genus the branch sheaths are promptly deciduous and fall away progressively as the leaf blades develop.

It requires no further analysis to make it clear that Ruprecht's description includes characters from at least one genus other than *Phyllostachys*. It cannot, therefore, be relied upon to clarify the specific identity of his type specimen if the specimen actually is a species of *Phyllostachys*.

But what of the type specimen itself? Immediately after the formal description Ruprecht cites a single specimen in words that, freely translated, say, "I have seen a Langsdorf specimen from Japan (apparently collected near Nagasaki)." The writer has not seen this specimen, but it presumably is still extant, along with the other material Ruprecht had before him, judging from the statements in the paragraph that follows the formal description. The type apparently consists of a sterile leafy branching specimen. No mention is made of flowers.

It is perfectly feasible to describe and identify bamboos on the basis of sterile vegetative material alone, *given adequate specimens of the critical structures*. It is only rarely, however, and in special cases, that a positive identification of a bamboo, or the differentiation of two closely related species, can be made on the basis of *sterile leafy branches alone*. That Koch, who transferred the specific epithet "reticulata" from *Bambusa* to the genus *Phyllostachys*, had an entirely erroneous idea of the nature of the latter genus is apparent from his comments that accompany the transfer (op. cit., p. 356–357).

Granted, however, for the sake of exploring the possibilities, that the Langsdorf specimen (Ruprecht's type) may represent a species of *Phyllostachys* (a group in which the *generic* determination can be made with confidence on the basis of adequate specimens of leafy branches) the specimen in question may be expected to represent one of the four species of that genus (all of Chinese origin) known to have been established in cultivation in Japan since early times. If the texture and dimensions of the leaves attributed to the specimen by Ruprecht in his diagnostic description are taken at face value, *Ph. pubescens* and *Ph. nigra* (including its forms) are ruled out, leaving *Ph. bambusoides* and *Ph. aurea* as possibilities. Here a critical complication arises. *Phyllostachys bambusoides* and *Ph. aurea* have very similar foliage. In recognition of this and other similarities (particularly in the inflorescence) of these two bamboos, Makino (Bot. Mag. Tokyo 11: 158. 1897) made the latter a variety of the former. Ohki, who made an exhaustive study of the systematic importance of spodograms in the leaves of Japanese bamboos (Tokyo. Univ. Fac. Sci. J. Sec. III Bot. 4: 1–130, *43 figs*. 1932) does not undertake to differentiate these two species by his method. However, to the writer, they are easily distinguishable by their culm sheaths and culm characters as well

as by their inflorescences. The writer considers them to be quite distinct species even though he is not able to separate them with confidence on the basis of sterile leafy branches alone.

The "reasonable doubt" mentioned at the beginning of this discussion focuses itself on the question, "Does the Langsdorf specimen, the type of *Bambusa reticulata* Rupr., represent the *Madake* of Japanese gardens, i.e. the plant known as *Phyllostachys bambusoides*, or is it something else?" The foregoing appeal to the available evidence leaves this question still unanswered. The reasonable doubt that clouds our view can be dispelled only by a positive identification of the Langsdorf specimen (connecting it with a known entity), supported by mention of one or more taxonomic characters by which it differs from comparable specimens of the other species with which it might be confused.

Current usage in Japan preponderantly favors the name *Ph. reticulata* (Rupr.) C. Koch for *Madake*, although Japanese taxonomists have offered no satisfactory documentation of their identification of Ruprecht's type. The preponderance of usage in Europe and the United States generally has favored the name *Phyllostachys bambusoides* for *Madake*. Until the type of *Bambusa reticulata* Rupr. can be shown to be unmistakably identical with this species, the writer can see no reason for displacing the well-founded name *Phyllostachys bambusoides* S. & Z. with the very inadequately documented *Ph. reticulata* (Rupr.) Koch.

The typical form of *Ph. bambusoides* is represented at the U. S. Barbour Lathrop Plant Introduction Garden by plants under P. I. 40842. This introduction is doubtfully reported (USDA Inventory of Seeds and Plants Imported, p. 89, *pl. vi.* 1915) to have reached this country via India, in 1890. Other introductions representing this typical form of the species are P. I. 12180 and 128787.

Phyllostachys pubescens Mazel ex H. de Leh., Bambou, p. 7 (Jan.) 1906; Nakai, J. Jap. Bot. **9**: 27–29, *pl. 6.* 1933 (excl. syn.)

Phyllostachys edulis H. de Leh., Bambou, p. 39 (Jan.) 1906. (not ? *Bambusa edulis* Carr., Rev. Hort. **37**: 380. 1866.)

Mosochiku of Japanese gardens.

Type: None cited. Neotype in U. S. National Herbarium, Nos. 2177859–60 (2 sheets), collected by *F. A. McClure* (No. 21800) April 17, 1955, from a colony cultivated under P. I. 80034 at the U. S. Barbour Lathrop Plant Introduction Garden.

Origin: China; introduced into Japan about 1737. (Satow, E. Asiat. Soc. Japan. Trans. 27(3): 35. 1899) ". . . In Europe it was confined until 1904 to the garden of the late M. Mazel at Prafrance, where it arrived around 1880, after the visit of the late M. Riviere." (H. de Leh. op. cit. p. 39)

In the United States the name *Phyllostachys edulis* (Carr.) H. de Leh.,

based on *Bambusa edulis* Carr., has generally been used for this plant. A translation of the original French description (Carr. loc. cit.) follows:

"*Bambusa edulis*; *B. mitis* hort. This species, the young shoots of which are said to be eaten as are those of hops, is a native of China. It is very vigorous and very hardy and belongs to the group *nudicaules*. Its characteristics follow:

"Stems erect, much branched, green. Bud sheath very large, soon becoming yellow; sheaths ciliate blackish, prolonged a little beyond the point of origin of the leaf blade. Leaves slender, very finely serrulate and almost ciliate on the margin, of a clear green above, glaucescent beneath, very long-acuminate at the apex."

Carriere left no type and supplied no illustration of this bamboo. From his very generalized and incomplete description one cannot, without making bold and unfounded assumptions, guess even the generic affinity of his bamboo, let alone its specific identity. The character "much branched" ascribed by Carriere to his plant excludes it from the genus *Phyllostachys* where the branches are paired at each node.

Houzeau's statement about the date of the first introduction of *Phyllostachys pubescens* into France by Mazel in about 1880 (op. cit. p. 9; see also quotation above in the paragraph beginning "Origin:") makes it extremely unlikely that this species was available to Carriere in 1866. The possibility that he may have had plants of it that originated from propagules of the heterocyclic form discussed below has been considered. However, this possibility also shrinks to extreme improbability when we consider the evidence.

Carriere did not describe *Bambusa heterocycla* until 1878, twelve years after he described *B. edulis*. If both the species and the heterocyclic form had presented themselves to his attention either simultaneously or contemporaneously, he would almost certainly have focused on the heterocyclic form first. His conspicuous record (Rev. Hort. passim) for bringing horticultural novelties to light in advance of their having been described by taxonomists supports this view. In any case, the original application of the name *Bambusa edulis* still remains uncertain.

In January, 1906, Houzeau (op. cit., p. 38) discovered that Japanese botanists had been applying the name *Phyllostachys mitis* A. & C. Riv. to the *mosochiku* of Japan, and that Makino's description of it (Makino, T., Bot. Mag. Tokyo **15**: 68. 1901) corresponded perfectly to the bamboo Houzeau himself had just described as *Ph. pubescens* Mazel (op. cit. p. 7). This discovery lead Houzeau to prepare an article, "Les deux Phyllostachys mitis" (op. cit. p. 38–39) in which he presented pertinent facts and made an adjustment in the nomenclature that he deemed appropriate. He was in a position to do this since he had in his collection living plants of the two bamboos involved; the true *Ph. mitis* A. & C. Riv., and the controversial *mosochiku* of Japan. The point of present concern is that Houzeau abandoned the name *Ph. pubescens* Mazel which he had just set up for the *mosochiku*, and substituted for it the new combination *Ph. edulis* (Carr.) H. de Leh.

An attempt is made in the following lines to reconstruct the mental process by which Houzeau was led to do this in the face of the demonstrated uncertainty of the application of Carriere's name.

Probably upon recognizing his *Ph. pubescens* in Makino's description under the name *Ph. mitis* he first re-read the Rivieres' description of *Ph. mitis*. Here he saw the synonym [*Bambusa*] *edulis* given. Although no authority was cited by the Rivieres for the name *edulis*, Houzeau probably was led to look up the original description of *Bambusa edulis* by Carriere. (He may have been influenced in this by the fact that Makino (loc. cit.) had given *Bambusa edulis* Carr. in his synonomy.) Carriere gives *B. mitis* as a synonym for his *B. edulis*. The psychological impact of this reciprocal citation of synonomy seems to have convinced Houzeau that he had discovered the reason why the two bamboos in question had become confused in the minds of the Japanese botanists. He seems to have been drawn irresistibly to the perfectly apparent solution: "If one of the two confused bamboos (both of which he had growing in his garden) is *Phyllostachys mitis* the other must be made *Phyllostachys edulis*!" He put this idea into effect at once. Unfortunately, in doing so he overlooked the implications of the fact he recorded earlier in the same article relating to the first introduction of *Ph. pubescens* into France about 1880 (*vide supra*). Evidently, however, he soon realized that his action in changing the name had been hasty, for he promptly reverted (op. cit. p. 55 et seq.) to the use of the name *pubescens* for the plant he had temporarily called *Ph. edulis*. This retreat from the use of the name *edulis* and the subsequent concurrence of Japanese usage are significant testimony to the fact that the application (content) of the name *edulis* is not satisfactorily documented, and still remains obscure.

In the light of the foregoing account, it is of interest to turn attention at this point to the fact that Lindley (Penny Cyclop. 3: 357. 1835) described, under the name *Bambusa pubescens* Loddiges, a bamboo "obtained by the English from the collections of France." The writer has examined a photograph of the type of *Bambusa pubescens* Loddiges ex Lindl. which is preserved in the University Herbarium, Cambridge, England. The specimen is only a sterile leafy twig but it is possible to assert with confidence that it clearly is not a species of *Phyllostachys* and so has nothing to do with *Ph. pubescens* Mazel ex H. de Leh.

Article 75 of the International Rules of Botanical Nomenclature (1952) reads as follows: "A name of a taxon must be rejected if it is used with different meanings and so becomes a long-persistent source of error." In the sense of Article 75 the combination *Phyllostachys edulis* and the name *Bambusa edulis* on which it is based appear to be *nomina rejicienda*.

A bizarre form of this species, the tortoise-shell bamboo, or *kikkuchiku* of Japan, known as the Lohan Chu in China, has been given taxonomic status as *Bambusa heterocycla* Carr., *Phyllostachys edulis* var. *heterocycla* (Carr.) H. de Leh., *Ph. pubescens* var. *heterocycla* H. de Leh. etc. Being based on a "monstrosity," however, these names must all be rejected. (Internatl. Rules Bot. Nomencl. Art. 77. 1952)

Phyllostachys viridis (Young) McClure comb. nov.

Phyllostachys sulphurea var. *viridis* R. A. Young, Wash. Acad. Sci. J. **37**: 345. 1937.

Phyllostachys mitis A. & C. Riv. Soc. Acclim. B. Ser. III **5**: 689. 1878, quoad descriptionem tantum; haud *Bambusa mitis* Poir. necque *Arundo mitis* Lour.

TYPE: ". . . deposited in the U. S. National Herbarium, nos. 1682470 and 1682471, collected in Plant Introduction Garden, Savannah, Ga., January 11, 1937, by *D. A. Bisset*; grown from material obtained in 1928 from Gaston Negre, Generargues, France, under the name *Phyllostachys mitis*." (Young, loc. cit.) This species is represented at the U. S. Barbour Lathrop Plant Introduction Garden by the original colony under P. I. 77257.

Origin: "China; introduced [into France] in 1840 by M. de Joncigny and in 1855 or 1856 by M. Montigny, French Consul at Shanghai, who is said to have imported it from Cochinchina." (Houzeau de Lehaie, Bambou, p. 39, 1906. Notes on *Phyllostachys mitis* A. & C. Riv. in an article entitled "Les deux Phyllostachys mitis.")

The above-mentioned reference to Cochinchina as a source of Montigny's plants probably is not well-founded, as no documented record of the occurrence of the species in Cochinchina has come to light. However, this reference to Cochinchina may have been what led the Rivières to take up the name *Arundo mitis* Lour. (Fl. Cochin. p. 57. 1790). On the basis of material collected in Annam by Dodo and Parrant, E. D. Merrill (Amer. Phil. Soc. Trans. **24**(2): 85. 1935) identifies *Arundo mitis* Lour. as a species of *Dendrocalamus*.

The name *Phyllostachys sulphurea* var. *viridis* Young is untenable because the name *Ph. sulphurea* belongs to a specifically distinct plant. The latter is treated elsewhere in this paper under *Ph. bambusoides* cultivar ALLGOLD (P. I. 89701). The plant (represented by P. I. 89718) misidentified by Houzeau (Bambou p. 99 et passim. 1906) as *Ph. sulphurea* becomes cultivar. ROBERT YOUNG of *Ph. viridis* (see p. 195).

HORTICULTURAL FORMS

The following entities that have heretofore been given taxonomic status as varieties or forms appear to belong in a more informal category, to which the term "cultivar" is applicable.

Phyllostachys bambusoides S. & Z.

CULTIVAR: CASTILLON

Reference to this entity will be found in the literature under the following botanical names: *Bambusa castilloni* Marliac ex Carr. Rev. Hort., **58**: 513. 1896. *Phyllostachys castillonis* (Marl.) Mitf., Garden **47**: 3. 1895. *Ph. bambusoides* var. *castillonis* Makino, Bot. Mag. Tokyo **14**: 63. 1900. *Ph. quilioi* var. *castillonis* H. de Leh., Bambou, p. 29. 1906. *Ph. nigra* var.

castillonis (Mitf.) Bean, Kew Bull., p. 232. 1907. *Ph. reticulata* var. *castillonis* (Marl.) Makino, Bot. Mag. Tokyo **26**: 21. 1912.

The CASTILLON bamboo is distinguished from the typical form of the species by the color pattern of the culms, culm sheaths, and leaves, as follows: Ground color of culm internodes (and branches) bright golden yellow (sometimes suffused with dilute wine in the lower part of the culm); the internodes of culms and branches show a broad green panel on the groove above each bud or branch insertion (and in analogous positions where buds or branches do not occur); culm sheaths have a greenish yellow background and a few green stripes. Occasional leaf blades show cream stripes. The ultimate culm size of this form is considerably less than that of the typical form of the species. CASTILLON differs from ALLGOLD principally in having the sulcus of the culm internodes green, and in having green striping always present outside the sulcus.

The colony of CASTILLON (P. I. 42659) under cultivation at the U. S. Barbour Lathrop Plant Introduction Garden is derived from plants purchased from the Yokohama Nursery Company, Japan, in 1916.

"This form is native to China. . . . It was introduced into Japan in the early days" (Nakai, T., J. Jap. Bot. 9: 240. 1933. Transl. Katsura, ed. R. A. Young. 1936). By 1886 it was established in cultivation in France (teste Carriere, loc. cit.). Tsuboi says that he found a culm of this bamboo (as a spontaneous mutation) in a forest of *Phyllostachys bambusoides* in Yawata-Mura, Gifu-ken, Japan (Illus. Jap. sp. Bamb. ed. 2, p. 6, 1916. Transl. Katsura, ed. R. A. Young. 1935).

Cultivar: ALLGOLD.

References to this entity will be found in the literature under the following botanical names: *Bambusa sulphurea* Carr., Rev. Hort. **45**: 379. 1873. *Phyllostachys sulphurea* A. & C. Riv., Soc. Acclim. B. Ser. 3, **5**: 773. 1878. *Ph. castillonis* var. *holochrysa* Pfitz., Deut. Dendr. Ges. Mit. **14**: 60. 1905. *Ph. quilioi* var. *castillonis holochrysa* Regel ex H. de Leh., Bambou, p. 118. 1908. *Ph. bambusoides* var. *castilloni holochrysa* (Pfitz.) H. de Leh., Congr. Internat. de Bot. 3. Actes **2**: 228. 1912. *Ph. reticulata* var. *sulphurea* Makino, Bot. Mag. Tokyo **26**: 24. 1912. *Ph. bambusoides* var. *sulphurea* Makino ex Tsuboi, Illus. Jap. Sp. Bamb. ed. 2, p. 7, *pl. 5*. 1916. *Ph. reticulata* var. *holochrysa* (Pfitz.) Nakai, J. Jap. Bot. **9**: 34. 1933.

ALLGOLD differs from the CASTILLON Bamboo in lacking the green panel on the sulcus of culm and branch internodes, and in having the green striping otherwise *very sparse, often lacking entirely*. The purely golden phase is the one illustrated by Tsuboi (loc. cit.). It is believed to be the one Carriere had before him when he described *Bambusa sulphurea* (loc. cit.) since he makes no reference to green stripes. Tsuboi (loc. cit.) mentions a plant of *Phyllostachys bambusoides* var. *sulphurea* he had in his own garden, "segregated from the roots of Ginmeichiku" i. e. from the CASTILLON Bamboo. This fact is interesting, and may be significant in view of the circumstance that plants of the bamboo here named ALLGOLD,

purchased by the U. S. Department of Agriculture from V. N. Gauntlett in 1930, were received under the name *Ph. bambusoides* var. *castilloni*. They are growing at the U. S. Barbour Lathrop Plant Introduction Garden under P. I. 89701.

CULTIVAR: SLENDER CROOKSTEM.

References to this entity will be found in the literature under the following botanical names:

Phyllostachys bambusoides S. & Z., illustrated as an abnormal culm. Tsuboi, Illus. Jap. Sp. Bamb. ed. 2, *pl. 58*. 1916. *Ph. reticulata* forma *geniculata* Nakai, J. Jap. Bot. 9: 34. 1933. *Ph. bambusoides*. Variety Slender Crookstem. USDA. Some bamboos growing at the U. S. Barbour Lathrop Plant Introduction Garden, Savannah, Georgia. Mimeo. p. 7, 1947.

SLENDER CROOKSTEM is distinguished from the typical form of the species by the occurrence, in a high percentage of the culms, of a curve (sometimes compound) near the base. The culms are often more slender in relation to their height than those of the typical form of the species; the culm nodes are generally less salient. Buds are borne at a lower level on culms of comparable size, and frequently more of the lower buds remain dormant than in the culms of the typical form of the species. There is often a more copious development of hairs on the culm sheaths, and these often develop on sheaths of culms of smaller size than in the typical form of the species.

Nakai's bamboo, described as differing from the typical form of the species in having more slender culms, of which the lowest part is "always zigzag" in form, appears to be the same as SLENDER CROOKSTEM now growing at the U. S. Barbour Lathrop Plant Introduction Garden under P. I. 146420. The plants under this number came from rhizomes secured in Kwangtung province, China, and sent to the U. S. Department of Agriculture by the writer in 1925.

Phyllostachys nigra (Lodd.) Munro

CULTIVAR: HENON.

References to the HENON Bamboo will be found in the literature under the following botanical names:

Bambusa puberula Miq., Mus. Bot. Lugd. Batav. Ann. III, 2: 285. 1866. *Phyllostachys puberula* (Miq.) Munro, Gard. Chron. (n. s.) 6: 773. 1876. *Ph. henonis* Mitf., Garden 47: 3. 1895. *Ph. nigra* var. *henonis* (Mitf.) Stapf apud Rendle, Linn. Soc. Bot. 36: 443. 1904.

The HENON Bamboo is, in all probability, the "biological parent" of *Phyllostachys nigra* itself and of all the entities associated with it in the literature as taxonomic varieties or forms. However, since the black-stemmed one was the first to be named (*Bambusa nigra* Loddiges ex Lindl., Penny Cycloped. 3: 357. 1835) it becomes the "taxonomic species" now called *Phyllostachys nigra* (Lodd.) Munro. The others (including the

HENON Bamboo), since they do not differ from it, or among themselves, in any morphological characters whatsoever, are, therefore, properly treated under that name as cultivars.

The HENON Bamboo is represented at the U. S. Barbour Lathrop Plant Introduction Garden by plants under P. I. 24761, 66787, and 75158.

CULTIVAR: BORY.

References to the BORY Bamboo will be found in the literature under the following botanical names:

Phyllostachys boryana Mitf., Garden 47: 3. 1895. *Ph. puberula* var. *boryana* Makino, Bot. Mag. Tokyo 14: 64. 1900. *Ph. nigra henonis* forma *boryana* Makino, Bot. Mag. Tokyo 26: 26. 1912.

The BORY Bamboo differs from the HENON Bamboo solely in the slightly smaller ultimate size of the culms of the former, and in their development during the first year or so of a few scattered, irregularly shaped dark spots on the lower internodes. The BORY Bamboo has a larger mature culm and its spots are much larger and spaced much farther apart than those of the typical form of the species.

The BORY Bamboo is represented at the U. S. Barbour Lathrop Plant Introduction Garden by plants under P. I. 77258, purchased from Gaston Negre, Generargues, France, in 1928.

Phyllostachys viridis (Young) McClure

CULTIVAR: ROBERT YOUNG.

This spontaneous, apparently stable mutant, here named the ROBERT YOUNG Bamboo, differs from *Ph. viridis*, from which it originated, in having a smaller mature stature and a distinctive coloration. The culms and branches are at first sulphur-green, with darker green stripes on the lower internodes and a narrow dark green band immediately below each sheath scar. The sulphur-green background gradually turns to old gold and the green stripes persist. The culm sheaths are slightly paler than those of the species, and occasionally show a slender green stripe or two. Occasional leaf blades show cream stripes.

The ROBERT YOUNG Bamboo is in cultivation at the U. S. Barbour Lathrop Plant Introduction Garden under P. I. 89718. Plants of it were received by the U. S. Department of Agriculture from V. N. Gauntlett & Co., Chiddingfold, Surrey, England, in 1930. No record of its introduction into Europe has been found. It could have appeared there, *de novo*, as a mutation from the species, whose introduction is recorded. The stock from which the Gauntlett plants came probably originated as a spontaneous variation in one of the introductions of the parent species from China. The ROBERT YOUNG Bamboo has been observed to originate spontaneously (personal observation, May, 1955) from propagating material of *Ph. viridis* in the nursery at the U. S. Barbour Lathrop Plant Introduction Garden.

Houzeau (Bambou, p. 57, 99. 1906) identified this bamboo as *Phyllostachys sulphurea* A. & C. Riv. On the strength of this identification Houzeau (op. cit. p. 214, *pl. 8*. 1907) made *Ph. sulphurea* a variety of *Ph. mitis* (= *Ph. viridis* [Young] McClure). His plant (here named ROBERT YOUNG Bamboo) is indeed a form of that species. However, the name "sulphurea" was misapplied by him. As pointed out by R. A. Young (Wash. Acad. Sci. J. 37: 344. 1937) the Rivières give *Bambusa sulphurea* Hort. (a name without standing) instead of *B. sulphurea* Carr., as a synonym of *Ph. sulphurea* A. & C. Riv. This may have been an inadvertency. In any case a comparison of the Rivières' description of *Ph. sulphurea* with Carriere's description of *Bambusa sulphurea* strongly suggests that the Rivières correctly believed they had the same plant that Carriere had.

The writer sees no reason for following Houzeau's interpretation of *Ph. sulphurea* since the original description of it does not apply to the plant he had. The material received by the U. S. Department of Agriculture under the name *Phyllostachys sulphurea* from Gauntlett is growing at the Barbour Lathrop Garden under P. I. 89718. Neither the description of *Bambusa sulphurea* Carr. nor that of *Phyllostachys sulphurea* A. & C. Riv. makes any reference to green stripes, though these are found on every culm of the ROBERT YOUNG Bamboo. However, both descriptions apply perfectly to the bamboo treated by Japanese botanists as a variant of *Phyllostachys bambusoides* S. & Z., and by the writer as a horticultural form of that species (see Cultivar ALLGOLD, p. 193 of this paper).

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ELMER DREW MERRILL

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RICHARD A. HOWARD

With portrait *

PROFESSOR ELMER DREW MERRILL, Arnold Professor of Botany, *emeritus*, and former director of the Arnold Arboretum, died on FEBRUARY 25, 1956, in the Lemuel Shattuck Hospital, Forest Hills, Massachusetts. Few American botanists were as well known or as widely honored as Dr. Merrill. Few, also, have published as much as he in his long and distinguished career as botanical administrator and research taxonomist. In a knowledge of the flora of Asia no one has equalled him and it is improbable that any future botanist can match his publications on the flora of that area.

Physically a man of slight build, Dr. Merrill's health was excellent and he often stated he never knew sickness until a short while after his retirement when he suffered the first of many strokes which were to cause his death. In early September of 1955 a severe attack ended his active career and caused him to be bedridden and paralyzed until his death five months later.

Many complete biographical sketches of Dr. Merrill have been published and in 1953 he published in the Asa Gray Bulletin the first part of his autobiographical memoirs with the promise of completion in later issues. Who's Who in America, American Men of Science and "Merrilleana," a volume of selections from his general writings which was published in his honor as a double number of Chronica Botanica, detail his career and his publications.

Elmer Merrill was born in East Auburn, Maine, in 1876. He entered the University of Maine in 1894 and an interest in biology supplemented by summer employment in the State Fish Hatchery replaced an earlier interest in engineering. He reports that his first collections of plant materials were inspired by Professor F. L. Harvey and that during his college career he amassed a collection of more than 2000 named specimens of all groups of plants which later were presented to the New England Botanical Club. Duplicates of these specimens were sent to the New York Botanical

* This portrait was taken in 1950 by Dr. Louis O. Williams in Honduras.

Garden in exchange for a copy of Britton and Brown's Illustrated Flora of the Northern United States and through these specimens an early contact with N. L. Britton was established. Following his graduation Merrill returned to the University of Maine as an assistant in natural sciences where, although no formal postgraduate work was offered, he "rounded out his college work," "gained additional experience" and followed his own "inclinations in the pursuit of systematic botany, although having little or no supervision." For these efforts Dr. Merrill was awarded an M.S. degree by the university in 1904, although he states "I can hardly claim that it was an earned degree." In later life Dr. Merrill was similarly rewarded for his accomplishments when he received honorary degrees of Doctor of Science (University of Maine, 1926, and Harvard University, 1936) and Doctor of Letters (University of California, 1936, and Yale University, 1951).

From 1899 until 1902 Merrill worked for the U. S. Department of Agriculture as assistant agrostologist, serving part of this time as assistant to F. Lamson-Scribner. Apparently none to satisfied with his chosen employment, he entered the Medical School of George Washington University, but during the first semester of his second year was offered a position as botanist with the Insular Bureau of Agriculture in the Philippines. His spartan boyhood stood him in good stead for the active career which followed, for his acceptance of this position and his arrival in Manila in 1902 marked the start of over fifty years of devoted study of Oriental flora. In the Philippines Merrill observed that the Bureau of Forestry was in greater need of the services of a botanist than was the Bureau of Agriculture and within a few months of his arrival in Manila he obtained a joint appointment to both bureaus. Thereafter he devoted his time to a study of the plant materials of the archipelago, spending approximately half of his time in the field collecting. Few government officials of his period and certainly only a few botanists since that time have visited as many parts of the islands as did Dr. Merrill. Identification of the specimens collected proved impossible with the library resources at hand and so over a period of years a remarkable library was built up under his guidance. To Merrill also must go the credit for starting the herbarium collections in 1902 which, by 1922, two years before the end of his Philippine service, numbered 275,000 mounted specimens. Merrill lived to see both this magnificent herbarium and library destroyed by the Japanese during World War II and lent his unfailing assistance in securing duplicate books and specimens to rebuild this collection.

Merrill states that on reaching Manila his ambition was the preparation and publication of a general flora of the Philippines. However, the number of plants known from the Philippines as recorded in published literature was 2500 in 1900 when Merrill started collecting and over 14,000 in 1923 when the team with which he worked, Copeland, Whiteford, Elmer and others, had completed their intensive collecting. Identifications were made first by trips to the garden and the botanical institution at Buitenzorg and later, during his periodic leaves, in the principal herbaria of Europe. In

view of the difficulties of identification and of handling such a complex flora, it is not surprising that Merrill's original ambition of a general flora was never acomplished. He laid the groundwork for such a flora, however, and through his efforts we have today a "Flora of Manila," published in 1914 and "An Enumeration of Philippine Flowering Plants," published in sections between 1923 and 1926, the latter with a total of 2143 pages. Professor Merrill's personal copy of his Enumerations (now in the library of the New York Botanical Garden) was carefully annotated with new records, changes in nomenclature and additional bibliography. As he worked with the flora of the Philippines and was exposed to flora of other island and mainland areas in Asia, Dr. Merrill recognized that a larger approach was needed for a proper interpretation and definition of the many species in the Philippines. Thus his interests, while still in the Philippines, spread to the phytogeography of the area, as well as the flora of China, Borneo and Guam as indicated in his published papers.

As his seniority in the Philippines increased and his abilities were recognized, Dr. Merrill was called upon for other duties. His knowledge was needed at the young University of the Philippines where he had an appointment as associate professor and later, head of the Department of Botany, in spite of a teaching load of eighteen to thirty-six hours a week. At the Bureau of Science during the absence of the director he served as acting director and in 1919 he became the director, serving in this capacity until 1923. In his autobiography Dr. Merrill describes fully his frustration at the heavy administrative load, which was unsought, and also noted his resentment of the tasks which conflicted with his real desires for taxonomic botanical work. His efforts as director of the Bureau of Science, supervising the research activities in fields other than botany, enhanced his background in agriculture administration and prepared him for the offer received in 1923 to become dean of the College of Agriculture at the University of California. His decision to leave the Philippines was apparently based on several factors; the lack of any degree of permanence or of retirement benefits in his positions, increasingly demanding administrative duties and the separation from his family. Merrill had married in Manila in 1907 and four children were born of this marriage, three in the Philippines and one in Washington, D. C. The Merrills' second son died in the second month of his life and thereafter Mrs. Merrill and the children lived in the United States while Dr. Merrill remained in the Philippines. One such separation lasted five years.

In 1924 he left the Philippines to embark upon a career which was to have a remarkable influence on American botany when he accepted the position as dean of the College of Agriculture. In his autobiography Merrill describes the magnitude of the task he had undertaken. He was in charge of a faculty of three hundred and fifty individuals, but knew only one or two members personally. He "succeeded an administrator whose policies, to a considerable degree, had failed." "Reorganization and the rebuilding of the *esprit de corps* of the staff was essential. The institution was overstaffed in relation to its material equipment." The staff was divided

physically as well as intellectually. The solution of these problems was made easier in 1924 when Merrill was appointed director of the Agriculture Experiment Station, as well, and in this joint appointment his recommendations for reorganization of the faculties, research program and physical resources were possible. Merrill spent six years in these positions and his success in the reorganization can be summarized in his own words and those of his successor. In his autobiography Merrill reports:

"I had met with a certain degree of success in my administrative work . . . and had the confidence of the agricultural community, the leaders in agriculture, the staff of the College of Agriculture and of the administration and staff of the University. I had been brought to California to consummate certain definite things and these had, to a high degree, been accomplished. The perplexing problems of the institution had to a large degree been settled; policies had been established which met with the very general support of the industry and the institution. The staff had been increased; the material equipment very greatly enlarged; the annual budget augmented (from $1,800,000 to $2,500,000). Important new buildings had been provided for the University farm on the Berkeley campus and at Riverside."

His successor at California wrote an appreciation of Merrill which was published in the California Countryman and stated:

"His quickness of perception, his unfailing patience and courtesy, his great store of common sense, his promptness in taking action, his approachableness and consideration for others have won for him the admiration and high esteem of his colleagues. . . . We of the University of California record not only our deep regret at losing him but also our profound appreciation of his remarkable contribution to the success and effectiveness of the program of the College of Agriculture of the scientific activity of the University in general, of our gratitude for the friendship and sympathy which he has shown his colleagues unfailingly and of the high regard we all entertain for him as a scholar, a scientist and above all a lovable human being."

In underlining his many accomplishments Hutchison refers particularly to the fact that Merrill was instrumental in establishing one of the best sets of curricula for colleges of agriculture and that he encouraged and stimulated in a sympathetic manner the prosecution of research on fundamental problems which underlie the science of agriculture.

Merrill's several reports as director of the Agriculture and Experiment Station and as head of the College of Agriculture tell little of his scientific work. Instead they dwell on the administrative problems of morale, growth, physical resources and financial requirements so familiar in such reports. Even during these years of heavy administrative and academic responsibility, Merrill's research and publications on the flora of the Philippines, China and Asia in general did not lag. As he states in his autobiography:

"I devoted all my spare time to actual work in systematic botany and in building up the oriental reference herbarium of the University. This work was all done outside of office hours and some idea of its extent may be gained by the

statement that in these exceedingly busy six years I added in excess of 110,000 mounted specimens to the University herbarium; in this time also I prepared and published one volume of 316 pages on the flora of Borneo and numerous shorter papers on the plants of China, Borneo and the Philippines. This work in systematic botany was indeed my safety valve, for once in the herbarium, whether early in the morning before my office opened, at noon, after office hours or on Sundays or holidays, I immediately forgot my administrative problems and during these many hours devoted to botany, became merely a botanist interested in botanical matters only. At such times I never concerned myself with the numerous pressing problems of the Dean of Agriculture."

It was also during this period that herbarium work allowed the formulation in Merrill's mind of aids and improvements to the techniques used. The early developments of his innovations of cardboard herbarium boxes, literature clippings, detailed field labels and arrangement of specimens from the Orient by related geographic areas date from his years at California.

In 1926 a movement was initiated to establish a botanical garden in Los Angeles and Merrill, originally a member of the Garden Foundation, the holding corporation, also served as its first and apparently only director. The California Botanic Garden at Los Angeles, some four hundred miles away from the College of Agriculture, occupied a considerable portion of Merrill's time, for in 1927 and 1928 he was officially spending four-fifths and one-half of his time, respectively, in this position. The garden was destined to last but a few years, for the economic crash and depression, as well as Merrill's transfer to the New York Botanic Garden, spelled the end to this garden of eight hundred acres. Actually it was an active garden, however, during Merrill's supervision, for an administration building and greenhouses were built, and approximately twelve hundred species of plants were growing in various sections. Established seed and plant exchanges, foreign and domestic, were recorded and a young library was started. Most indicative of Merrill's hand, however, is the fact that in its brief existence the California Botanic Garden amassed an herbarium of 180,000 mounted specimens which, upon dissolution of the Garden, were transferred to the University of California at Los Angeles.

Merrill was approached in 1927 by officials of the Board of Managers of the New York Botanical Garden to determine whether he would be interested in becoming director of the latter organization following the retirement of Dr. N. L. Britton. In July of 1929 the matter came to definite form when the Board of Managers of the New York Botanical Garden held a special meeting to accept the resignation of Dr. Britton and Merrill reports that he learned of his appointment subject to his acceptance from an Associated Press dispatch in the San Francisco Chronicle. He also writes of personal family reasons for the change he was to undertake and comments, "If one were looking merely for power, one would not make the change, for the administration of an annual budget of $2,500,000 in a dynamic and rapidly expanding institution was in sharp contrast to the administration of less than one-fifth of that amount in an institution that had

become almost static." The move apparently was not without regrets, for writing in 1930 from New York Merrill states:

"History repeats itself, in that frequently I have questioned my judgement in accepting my present position. As in California during my first year or two there I looked back to Manila with keen regrets that I had ever left that city, so I frequently look back to the University of California and wonder why I ever left such a dynamic, progressive, expanding institution to cast my lot with an institution that was practically static, very badly under-financed and more or less under fire for its past policies and accomplishments. To rebuild the *esprit de corps* of the staff of one institution with reasonably ample and increasing financial resources is one thing; to attempt the same thing in another institution with totally inadequate financial support and little prospect of its increase is another."

Merrill's move from the University of California to the New York Botanic Garden took place at the start of the long economic depression of 1929–1934. Perhaps his laments of 1930 as well as his actual decision to move are involved in the financial adjustments necessary in both organizations. The New York Botanic Garden was supported by funds from private endowment and in part by financial support of the city of New York. The University of California, in particular the College of Agriculture, depended on state aid. It is interesting to note that much of Merrill's success at the New York Botanic Garden depended directly on the existence of a major economic depression. In a published tribute when Merrill resigned in 1935 the Board of Managers of the New York Botanic Garden noted "in particular the promptness and foresight with which he secured for the garden the assignment of workers and appropriations of funds by various emergency relief and employment bureaus for general assistance and much-needed repairs and improvements." During the depression years the New York Botanic Garden, like many organizations of its kind, was in serious financial difficulty. Not only was the income from endowments reduced but appropriations from the city, which were the source of the labor to maintain the grounds and wages of the professional staff in the herbarium, as well as supplies such as fuel, were severely cut. In his annual report for 1933, Merrill describes the difficulties of operating the Garden on a reduced appropriation of twenty percent as compared with 1931 and the fact that capital had been expended for several years and repayments had to be made from current income.

The details of how Merrill secured assistance from public relief agencies are not known, but his annual reports while director of the New York Botanic Garden indicate the scope of financial backing ($183,000 in 1934) which he acquired for untrained and semi-trained personnel to work in the garden and the herbarium. His reports indicate both the number of people to be supervised and the nature of the work accomplished. From the horticultural point of view it was in this period that major developments were made on the grounds of the garden. Walks were laid, roads developed, a rock garden constructed, fences built and floral displays organized and re-

organized. Appropriations from the Emergency Work Bureau and the Civil Works Administration allowed the employment of an average monthly total of eighty men in 1931, ninety in 1933 and one hundred fifty in 1934.

Women, skilled and unskilled, were available on emergency relief funds for work inside the building as mounters, artists, secretaries, librarians, clerks and technicians. In his reports Merrill speaks of seventy to ninety women employed in the herbarium and laboratories and in 1932 states the value of this assistance:

"It is impossible in this brief report to indicate in detail what this has meant to the progress of the work of the New York Botanic Garden and what it has meant to the individuals who have been given employment. It has, however, served to indicate how understaffed the New York Botanic Garden is in reference to what it is attempting to do, a fact that has long been known to the Board. The very fact that so many individuals could be employed throughout the year for productive work that has long required attention brings this situation into rather sharp relief. The employment of over three hundred individuals, with an average of over one hundred twenty per month throughout the year, has, of course, entailed distinctly heavy burdens on staff members who have had to supervise this work."

The accomplishments of this tremendous herbarium staff under Merrill's direction are indicative of the active mind of the administrator. Here was an opportunity to do herbarium work which had never existed before and which probably will never be duplicated. There was no accurate count of the total number of specimens in the herbarium of the New York Botanic Garden, so emergency labor undertook this task and a total figure was published for the first time in 1934. When the backlog of specimens in the herbarium at New York was depleted, specimens were mounted for other organizations. Merrill reports that twelve thousand specimens were mounted for the Gray Herbarium, the Arnold Arboretum and the Philadelphia Academy in 1934. Repairs were made on sheets in the New York herbarium and specimens mounted increased to 70,150 in the same year.

It was at this time, with adequate labor at the disposal of the staff, that Merrill exploited an earlier idea of placing in the herbarium proximate to the appropriate specimens, literature pertaining to those taxa. Type descriptions were copied from the literature, photostats were made and reprints cut up and the descriptions were attached either to the inside of the genus cover in the case of keys to genera and generic descriptions, or on species cover sheets for species and subspecific categories. Typists unskilled in herbarium work could prepare these descriptions and all were proofread before insertion. In the year 1934 over one hundred thousand such sheets of descriptions were added to the herbarium. In 1937 Merrill estimated that the total number of descriptions added to the herbarium at the New York Botanic Garden was "over 700,000 and it may well be greatly in excess of that number." As duplicate copies were made of all typed descriptions, the carbons were sent to other herbaria. The work continued after Merrill left New York and for many years after his arrival

at the Arnold Arboretum, he received thousands of these duplicates for insertion in the herbarium at the Arnold Arboretum.

Needless to say, the addition of seventy thousand specimens and one hundred thousand descriptions in one year crowded the standard herbarium cases and the cardboard herbarium boxes developed at California were pressed into use. Spare floor space in the herbarium was piled with these boxes as temporary housing for herbarium specimens and other boxes were piled many rows high on the top of standard cases.

In an annual report summarizing the last year Dr. Merrill was at New York, M. A. Howe reported:

"The herbarium has been growing with unabated activity. Besides the pasting in of many thousands of clippings and copies of original descriptions and cleaning and repairing specimens, 53,954 specimens have been actually added during the year. It is of note that nearly half of these additions represent Oriental specimens sent to Dr. Merrill for identification and that with the departure of Dr. Merrill, accessions from the Orient will suffer a corresponding shrinkage. Since a rate of growth similar to this has been in progress for somewhat more than five years, our herbarium cases have become full to their limit, or nearly so. We have in use at the present time more than 3,000 temporary cartons of corrugated paper in which all of our oriental material is stored. The replacement of these paper boxes alone will require about 60 standard herbarium cases and the future growth of the herbarium for the next decade may be conservatively estimated at 70 additional standard cases."

Another development possible with the surplus of labor on emergency work relief was the alphabetized series of entries for Index Kewensis. Merrill, years before, had seen the system of entries in Index Kewensis used at the Royal Botanic Garden, Kew, England, where the Index Kewensis is compiled and also at the herbarium in Leiden. The convenience of finding sequential entries in contrast with searching in as many as fifteen places in Index Kewensis was a definite advantage in herbarium work. Two teams of four women accomplished the task of cutting and pasting two copies of Index Kewensis in Moore loose-leaf binders. The finished books contained 2,457 pages and the labor cost was in excess of two thousand dollars.

Merrill's accomplishments at the New York Botanic Garden were great. However, he realized that the financial resources of the organization were not extensive and that the bonanza of relief labor would not last forever. He expressed this feeling in his annual report in 1932 when he stated:

"The outside plants should and must be improved preserving at the same time a definitely balanced program between scientific and horticultural work, a program however difficult to establish on the basis of our present restricted income. The New York Botanic Garden annually devotes about two-thirds of its income to maintenance and garden work, and one-third to the support of its scientific activities — just the reverse of the situation in other institutions with which we might be compared."

In 1935 Merrill received an invitation to join the staff of Harvard University as "Administrator of botanical collections." His task to ad-

minister the activities of eight and later nine separately endowed units in the field of botany. A named professorship, the Arnold Professor, was his and a recent drive had raised over one million dollars to increase the endowment. The job was indeed a challenge but this time the financial resources were greater and it appeared the task could be accomplished where a small fraction of the income need be devoted to horticulture and the large majority of funds were available for scientific work.

Merrill transfered to Harvard in the sixtieth year of his life. While he had earlier questioned in his autobiography the wisdom of changing positions at his age when he left California, he accepted the Harvard position with the understanding he would work past the normal retiring age of sixty-six until the age of seventy. Merrill actually retired at the age of seventy-two, one of only thirteen Harvard professors in the last quarter-century who were permitted to work beyond the age of seventy. Merrill therefore had ten years to accomplish the goals he outlined in his first annual report as administrator of botanical collections at Harvard. In retrospect the nature of his accomplishments speaks strongly for his abilities as an administrator and a scientist.

The position of administrator of botanical collections was created at Harvard in 1935 and Merrill was the first occupant of the post. He states "the objectives were to coordinate the work of several independently endowed units, to eliminate unnecessary duplication where possible and to integrate further the work of these units with the operations of the Department of Biology of the University." As Merrill points out:

"Professor Ames as chairman of the council of botanical collections had initiated and consummated many reforms affecting the separately endowed units. He logically abandoned the policy of isolation practiced by several of the units and adopted a new one involving closer cooperation and coordination of the work. His pioneer work established harmonious relationships between the several units in the division of biology to the advantage of biology as a whole."

Merrill's plans were to continue these interrelations with the other botanists and biologists of the university and to consolidate the physically and often intellectually separated activities. Merrill felt physical consolidation was most desirable and reports:

"It is eminently desirable that some consolidation eventually be effected but if and when this can be done depends upon a number of factors. It is a fact that Harvard University maintains three of the largest botanical libraries in America and three great herbaria. There is thus a very considerable and unavoidable duplication in purchases of both reference material, books, subscriptions to periodicals and a considerable amount of duplication of the library situation. Could some equitable plan of concentration be developed whereby the three libraries and three herbaria could be assembled in one building very material savings could be affected in maintenance charges as well as in the operation of the herbaria and the libraries. With such a change a single library would serve all three herbarium units. Such a plan would be of inestimable advantage to the three units involved not only to the elimination of duplication and even triplica-

tion but in greatly increasing the efficiency of the staff members of the now physically separated units."

Merrill's proposed solution to this was presented in his first annual report and he worked hard towards this goal throughout his years as administrator of botanical collections. His solution to problems of expansion and growth was not additions to the Administration Building of the Arnold Arboretum in Jamaica Plain and to the Gray Herbarium building in Cambridge but abandonment of these units which were to be reestablished in one central building. In 1936 he states:

"if additions be made to the two present buildings, about seven miles apart, the present unsatisfactory situation will be perpetuated. It is hoped that some practical plan of concentration can be developed thereby the herbarium and library facilities of the Gray, the Arnold and the Farlow may be concentrated in one locus."

Merrill referred to the disadvantages of the separation in all of his official reports. The strength of his feelings was emphasized in his choice of words referring to the botanical entities. "Unsatisfactory and inefficient," "can only result in stagnation and decline of productive output" "duplication or even triplication," "thoroughly unnatural, unnecessary and expensive physical separation of the library and herbarium facilities" "duplicating, triplicating and in some cases quadruplicating library purchases" are phrases often repeated in his reports.

Merrill's entreaties did not fall on deaf ears and in 1938 he apparently received an indication he should formalize his plans for a future move. With members of the Arboretum staff and through consultation with members of the organizations to be involved discussions were held and plans were drawn up. Complete blueprints of the new building were made in the summer of 1939. This building was to be located as Merrill had proposed in his reports in Cambridge between the Biological Laboratories and the Museum of Comparative Zoology and would necessitate the demolition of the Farlow Herbarium Building.

The idea, reported Merrill:

"is to bring together in one place not only the extraordinary library and herbarium facilities of the Gray, the Arnold and the Farlow but also as to the library the enormous collections of the Museum of Comparative Zoology thus forming a single comprehensive biological library. The logical place for this development is contiguous to the University Museum and the Biological Laboratory in Cambridge. This one great library would then serve all the biological needs of the University and would form a great collection of reference literature vastly superior in size and content to any similar collection of published biological data in America. . . . The ideal is one building sufficiently large to house adequately the existing reference collections of the botanical libraries and to allow for reasonable expansion. Such a consolidation would immensely increase the efficiency of all the units involved, reduce maintenance expenses, expedite the work of staff members and release for exchange or sale a vast amount of duplicate material that would no longer be needed here."

The building Merrill and his committee planned was never named although possible honors were discussed. The building was to house the collection of glass flowers on the first floor. One wing of the building was to house the combined libraries of the Arnold, Gray Herbarium, Farlow Library, Museum of Comparative Zoology and the Ames Orchid Herbarium and Library on five full floors and three additional half floors and these would occupy over 24,750 square feet of floor space. The major portions of three floors would be utilized as herbarium space. Only two offices were planned in the building for the staff was to occupy tables in the herbarium following the systems then in use at both the Gray and the Arnold. The facade of this very modern building would bear the names of Arnold, Gray and Farlow and the building could be built and equipped for less than one million dollars. In the fall of 1939 the international situation worsened with the outbreak of war in Europe and the concomitant restrictions imposed in the United States. It was soon apparent that construction of a major building at that time was impossible and unpatriotic. Thus the well drawn plans for consolidation of botanical resources at Harvard were laid aside for the duration of the war.

Merrill began his career at Harvard with an office in the Gray Herbarium building in Cambridge. His personal concern however was the administration of the funds of the Arnold Arboretum and only the supervision and coordination of activities of the eight other privately endowed institutions. After the first year he transferred his headquarters to Jamaica Plain when the University acquired a residence for the director of the Arnold Arboretum which appended the grounds. Merrill lived in this house on 960 Centre Street until the time of his death. This residence became a mecca for visiting botanists who at the same time could be within one hundred yards of the Administration Building with its fine herbarium and the famous collection of trees and shrubs on the grounds.

To assume responsibility for horticulture and the care of the grounds Dr. Merrill added for the first time the position of "Horticulturist" to the staff of the Arboretum, and the horticulturist, assisted by the propagator and superintendent of buildings and grounds, assumed the responsibility for the living collections allowing Merrill to devote his undivided attention to the herbarium and library and his personal research on Asia. The interest of the Arboretum in the flora of Asia dated from the period of Sargent and reflected especially the field activities of E. H. Wilson. Wilson was a botanical collector with an eye of appreciation for the potential ornamental trees and shrubs of the area. Wilson collected herbarium specimens for vouchers of the seeds and for more detailed study of the plants considered useful as ornamentals. Wilson had died before Merrill's appointment at Harvard and in his first year, with sufficient funds for such activities Merrill began a program of field work, supporting native botanists in their home area with small grants of money to enable them to collect specimens and to send seeds of the most promising ornamental plants seen. The initial grants went to Chinese botanists but eventually support was extended to botanists in Japan, Korea, the Philippines and in fact most areas of

Asia where botanists existed. During two years of Merrill's administration as many as fourteen botanists and institutions were conducting field work subsidized by the Arnold Arboretum. The number dropped during the war years and increased immediately afterward. It wasn't long before the specimens began to arrive at the Arnold Arboretum. Some were identified, but the majority were not. In this situation Merrill was at his best. Few botanists could match Dr. Merrill in "spot" identification of material from Asia and it was a rare plant which was not immediately analyzed with a selective eye and placed in the proper genus and family or if too common promptly discarded. Those selected for further study went promptly to the mounters and the number of specimens prepared for insertion in the herbarium increased. Space to house these specimens soon became critical for the new additions soon outgrew the space available in the standard herbarium cases. Once again Merrill resorted to the cardboard herbarium cases developed at California and used again at New York to meet the same situation of rapid expansion. Display rooms for museum collections open to the public soon were pre-empted for herbarium storage and every nook and cranny began to hold cardboard herbarium boxes of specimens.

In the herbarium proper Merrill introduced the ideas he had developed earlier at New York and California. Ten phytogeographic areas were designated with a different colored folder for each area. The organization of this system in a herbarium of half a million specimens was a major undertaking for the botanists on the staff.

The Arboretum possessed copies of Index Kewensis and here again Merrill carried out the alphabetization of entries which had been done at New York with emergency labor funds and relief workers. The principal difference was that at the Arboretum the work was done by the professional botanists on the staff.

The system of clippings begun at New York was also continued by Merrill on his arrival at Harvard. Perhaps foresightedly Merrill had had carbon copies prepared and while some of these were sent out gratis from New York Merrill formalized the agreement while at Harvard and helped support a continuation of this work at New York with the originals coming to the Arnold Arboretum. While it is true these clippings save an enormous amount of work and decrease the necessity of going to the library for original descriptions their method of insertion began to add to the bulk in an already overcrowded herbarium. The species covers with the attached descriptions were often thick. In many cases both genus and species covers were prepared for descriptions where there were no specimens. In other cases several sheets of paper were involved for species reduced to synonymy and so descriptions were filed in two or more places in the herbarium. Various measures were taken to relieve temporarily the congestion present in both the herbarium and the library. More American material was transferred on semi-permanent loan to the Gray Herbarium, thereby increasing their problems of handling and storing the specimens. The orchids were transferred to the Ames Herbarium in the botanical museum. A large col-

lection of books dealing with forestry were transferred to the Harvard Forest in Petersham, Massachusetts. Some of the older pre-linnean works were transferred for more satisfactory protection to the rare book library of Harvard. Within the herbarium proper there was absolutely no room for insertion in sequence of newly mounted materials and so a second family sequence was started on the tops of the steel cases by storing mounted sheets in cardboard cartons. Tables and alcoves formerly used by staff and visitors were confiscated for specimens. Display materials were stored in the barn and the collection of wood specimens and slides were moved to space in the biological laboratories in Cambridge.

Each innovation while improving the usefulness of the herbarium proved expensive, in the cost of professional staff time for the work, in the materials and in compounding the already crowded situation in the herbarium.

In the meantime at Harvard Merrill's research on the floras of Asia increased. Horticultural work caring for the grounds and meeting the public was adequately handled by the new horticulturist. Identifications of horticultural plants were the interest of Alfred Rehder. Funds for the first time in Merrill's career were adequate for taxonomic research and purchase of specimens or support of foreign collectors and as the new collections were studied his personal production of scientific articles jumped.

Using the extensive library resources of the Arboretum he published alone and with co-authors a "Polynesian Botanical Bibliography" of 194 pages and a "Bibliography of Eastern Asiatic Botany" of 719 pages He maintained and increased his bibliographies of the Philippines and for other island areas which unfortunately were never published.

His interest in validating botanical names led him to study critically the descriptions of older and often ignored botanical publications. The work of Otto Kuntze on plants from Indo-china, Palisot de Beauvois. Houttuyn, Muhlenberg and Rafinesque on plants from America revealed many combinations unrecorded in Index Kewensis which affected the nomenclature of plants from America as well as Asia. Feeling strongly that these works should be consulted more frequently but recognizing that the volumes were rare and unavailable Merrill instituted a technique to reproduce many of these rare volumes by lithoprint. The copies in the library of the Arnold Arboretum were used in the process but the work was financed largely through private funds supplied by Dr. Merrill.

The specimens in the Linnaean herbarium were also considered by Dr. Merrill to be too inaccessible to most American botanists and he encouraged the recording of these specimens and their available data on microfilm. This was accomplished during the war years through a grant from the Carnegie Foundation. When the Arnold Arboretum received these microfilms Dr. Merrill had 5×7 glossy prints made of each and mounted on stiff cards approximately twice that size. The complete data from Savage's catalogue was printed with the photograph and together these data form a valuable research tool.

His taxonomic interest turned to New Guinea with the prospect of an expedition visiting that area and in 1936–1937 the Arnold Arboretum sup-

ported financially the botanical efforts of the second Archbold Expedition to that immense island. All of the specimens collected by the botanists were sent to the Arboretum where the collections were studied, labels prepared and the duplicates distributed. The same arrangements were made with successive expeditions to the area and in these plant collections came close to a thousand plants new to science. As co-author with Dr. Lily Perry of the Arboretum staff there began in the Journal of the Arnold Arboretum the series, "Plantae Papuanae Archboldianae" of which Number 18 was published in 1949.

Merrill's familiarity with the Pacific Islands and the vegetation of that area proved of great value during the war years. He was frequently called to Washington for consultation and the full record of his service will probably never be revealed. In 1945 he was the recipient of the Appreciation Certificate for his services as Consultant to the Secretary of War. With the assistance of Mr. Gordon Dillon on the art work, Dr. Merrill compiled a handbook of the "Emergency food plants and Poisonous plants of the islands of the Pacific" which was published by the government as a War Department technical publication. The illustrations and the text of this booklet were reproduced in many of the survival manuals issued by the branches of the military service. In this publication Dr. Merrill's personal experience as well as the excellent library and herbarium resources of the Arnold Arboretum were evident. This book remains extremely useful to the botanist for the compilation of local and dialect names for the common plants of the Pacific Islands. As part of the education program for our troops in the Pacific theatre several books on wild life and natural history were published. Dr. Merrill contributed the material on plants in "The Pacific World" which was edited by Fairfield Osburn and later wrote the more comprehensive "Plant Life of the Pacific World" which was published with hard covers by the Macmillan Company and in a pocket and paper cover edition by the Infantry Journal as one of the Fighting Forces editions. In these booklets Dr. Merrill described the technique for collecting plants as scientific records of the vegetation of the area. In response to many inquiries Dr. Merrill was always encouraging, and correspondents wherever they might be stationed were invited to send plant specimens in for determination. With the assistance of other members of the Arboretum staff these plants were identified, some interesting facts about the collection or the taxon related and the determination promptly returned. Many commanding officers and postal censors considered such activities as violation of security regulations and many shipments of specimens were confiscated and sent to government agencies or destroyed.

When the war in Europe ended and it appeared only a matter of time before hostilities in the Pacific would be over Dr. Merrill renewed his requests for a consideration of the problems of the herbaria and libraries he supervised. The continued increase in the Harvard University herbaria during the war years had completely filled all available space and the libraries were overflowing the shelf space available. Dr. Merrill suggested that the plans for a consolidation and the construction of a new building

which had been drawn up and tentatively approved in 1938 and 1939 should be reviewed for quick action once the war was over and building restrictions lifted. In 1944 Dr. Merrill was sixty-eight years old, three years beyond the normal age at which professors are normally freed of administrative duties and two years beyond the normal retirement age. In view of Dr. Merrill's expected retirement at age seventy, the Provost asked Professor I. W. Bailey, professor of wood anatomy on the staff of the Arnold Arboretum and senior botanist in length of service to Harvard, to review the previously drawn plans and submit a confidential report. This report entitled "Botany and its applications at Harvard" was written with the consultation and advice of the botanists in the many botanical institutions at Harvard and was approved by them all. Dr. Merrill moved for the acceptance of this report at the faculty meeting where it was submitted and Dr. Fernald, then director of the Gray Herbarium, seconded the motion. The report was approved on March 1, 1946, by the President and Fellows in their joint role as Administrators of Harvard College and Trustees of the Arnold Arboretum. The program proposed repeated Merrill's call for the erection of a single building to house the herbarium and library collections of the several botanical institutions at Harvard, as well as some administrative changes. The new building was to be in the location proposed earlier by Dr. Merrill but would not be as all-inclusive as he had originally visualized, for it did not seem practical to house the libraries of the Biological Laboratories and the Museum of Comparative Zoology in one unit. However the combination of libraries and herbaria proposed would reduce the duplication of purchases and expenditures, provide new and larger quarters and allow room for expansion and bring staff members of similar interests in closer association for mutual benefit.

Construction of the new herbarium building was delayed until wartime restrictions on building were lifted and in the meantime further discussion of the proposed administrative reorganization took place. The new building was finally erected in 1953 and occupied in 1954, eighteen years after it was first proposed by Dr. Merrill.

When Dr. Merrill was no longer involved in the affairs of administration of the Arnold Arboretum he directed his attention full time to his research. The contacts which he once had had with botanists in Asia were reestablished and supported by grants from the Arboretum and these men again began to send collections for Dr. Merrill's attention. Special mention should be made of the efforts of Dr. Merrill to supply his botanical friends with the necessities as well as a few of the luxuries of life in their post-war existence under rationing restrictions. To Asia and to Europe Dr. Merrill directed packages he himself prepared. His contributions in the form of CARE packages will never be forgotten as an indication of his extreme concern and generosity for his friends.

One botanical expedition in China collecting for the Arnold Arboretum located fruiting trees of *Metasequoia* which Merrill described as another "living fossil." This exciting discovery opened a new vista and Dr. Merrill became a modern "Johnny Appleseed," for he acquired several bushels of

these seeds which he distributed widely for trial. At one European horticultural meeting Merrill made a lasting impression by appearing on the speakers' platform his pockets bulging with what proved to be the seeds of this most unusual plant. His interest in the distribution and the success of this introduction lasted until his death.

Dr. Merrill had been on the selection board of the Guggenheim Foundation for many years and contributed valuable service in the screening of the many applications. In 1951 he in turn was the recipient of a grant, the first of several grants from the Foundation which enabled him to spend six months in Europe where he visited many of the major herbaria. He examined many of the types of Asiatic plants, making critical notes and carbon paper tracings. At the British Museum he worked over and identified many old collections and selected for the Arboretum a number of available duplicates of the Carr collection from New Guinea. At Brussels he critically studied the Roxburgh specimens in the Martius herbarium and prepared a list of the plants and their identifications. Carbon copies of this list were sent to the several institutions maintaining an interest in such Asiatic collections, but unfortunately the data have not been published. It was unfortunate that Dr. Merrill suffered another severe heart attack while on this European trip and from that time on was advised to limit his activities and restrict his travel. It meant that he had to give up his winter trips to Cuba, Honduras and Panama and he found the New England winters more difficult to endure. His thoughts remained in the tropics, however, and he reacted violently to some well-publicized theories of transpacific migration of plant materials involving raft travel and human agencies. The problems of distribution of American crop and weed plants in the Pacific and Asiatic plants in the western hemisphere had long been of interest and concern to him. As early as 1904 he had published on "The American element in the Philippine Flora" and at the end of the war he investigated the species introduced in the region of Manila by military activities. His last few years were spent in examining the manuscript records of the early expeditions to the Pacific islands. His observations and opinions were expressed in typical Merrillian fashion in his final publication, "The botany of Cook's voyages and its unexpected significance in relation to anthropology, biogeography and history," published by Chronica Botanica in 1954.

Merrill is survived by his widow, Augusta Sperry Merrill and one son, Dudley. His ashes are to be interred in a family plot in East Upton, Massachusetts.

In retrospect only one word can satisfactorily describe Elmer Drew Merrill and his contributions to the knowledge of botany. He was a builder. His handiwork is evident in many parts of the world. In herbaria alone Merrill must receive credit for amassing outstanding collections. The two thousand specimens collected as a student at the University of Maine were given to the New England Botanical Club. In the Philippines he began the herbarium of the Bureau of Science which in 1922, two years before his departure, contained two hundred seventy-five thousand mounted

sheets. At California, herbarium accessions in the two years before Merrill's arrival averaged 8,250 sheets but swelled from 27,000 to 37,000 sheets a year during and immediately after his administration. His own estimate of the increase in the herbarium at the University of California during his stay there was 110,000 sheets. During the short period of his directorship of the California Botanic Garden an herbarium was started and built up to over 180,000 sheets. From 1930 to 1935 Dr. Merrill, as director of the New York Botanical Garden, increased the herbarium under his supervision by over 280,000 mounted specimens and to this must be added the insertion of over 700,000 sheets of descriptions of plants. At Harvard, too, the herbaria felt his influence, for the herbarium of the Arnold Arboretum, founded in 1872, increased over fifty percent in size during the term of his directorship, from 409,000 to 631,000, while at the same time, in excess of 130,000 sheets were transferred to the Gray Herbarium, the Farlow and Ames Herbaria. Thus, one man has accounted for the amassing of botanical resources totalling over one million sheets of herbarium specimens and untold numbers of duplicates distributed for the benefit of the botanists to follow him.

Our path has been made clearer by his keen mind and his extensive record of publications. Nearly five hundred titles are credited to his pen, for he published one hundred forty-five significant papers and books on the flora of the Philippines, fifty-four on China, thirty on New Guinea and more than a dozen each on islands such as Sumatra, Borneo and Java. His desire for simplification in the citation of technical journals led to the adoption of one-word titles for periodicals such as Brittonia and Sargentia, which he helped create, or Hildgaardia and Arnoldia, which replaced more cumbersome names. While he had few students to carry on his work, his influence of position and personality carried respect and won for him many times the honor of having his name associated with a living plant. The genera and species named by him number more than a thousand and those named for him are more than a dozen. *Magnolia* "Merrill" carries his name in the north, as does the Merrill Palm (*Adonidia merrilli*) in the tropics.

It can be said with respect and appreciation that he made his immortality through the plants that he loved.

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A MONOGRAPHIC STUDY OF THE WEST INDIAN SPECIES OF PHYLLANTHUS *

GRADY L. WEBSTER

With twelve plates

LEAF

Lamina.

The leaf-blade in *Phyllanthus* (and in the other genera of Phyllantheae as well) is invariably simple and entire, but there are many variations of size, shape, and texture. In a few species such as *P. urinaria* and *P. carnosulus* there may appear to be a minutely serrate or crenate margin, but this appearance actually is due to projections of individual or associated epidermal cells which belong in the category of trichomes; true vascularized teeth never occur.

The leaf of *Phyllanthus* varies in size from minute, as in *P. imbricatus* where it may be only 1.5 mm. long, to large as in *P. grandifolius* where it may attain 15 cm. in length and almost as much in width. It is not surprising that the leaves of *P. grandifolius*, which are borne on permanent branches, are large and persistent; but a few species, such as *P. juglandifolius* and *P. cornifolius* with the foliage leaves only on deciduous branchlets also have leaves 15 cm. long, although never as broad. On the whole, the leaves of *Phyllanthus* are medium-sized or small, and the median for the genus would perhaps fall at about 3 cm.

Most species of *Phyllanthus* have elliptic to oblong leaves, but as might be expected in so large a genus, there are some striking deviations. In some New Caledonian and South American species (e.g., *P. bupleuroides* and *P. duidae*) the lamina is prominently basally lobed and has the outline of a *Cercis* leaf-blade. A few xerophytic species such as *P. comosus* and *P. formosus* (sect. *Orbicularia*) have leaves with a pronounced spathulate outline. The apex of the blade varies from retuse to acuminate among various species, and in some of the Cuban species of sect. *Orbicularia* there is a long attenuate scarious tip, which however is differentiated from the rest of the leaf-blade. A pronounced "drip-tip" such as characterizes the leaves of many Lauraceae in the tropical rain forest is scarcely developed in any species of *Phyllanthus*.

Leaf texture within the genus runs the gamut from extremely tenuous and delicate as in *P. tenuifolius* (sect. *Cyclanthera*) to rigidly coriaceous in species of several sections (e.g., *Orbicularia*). The leaf surface is usually smooth, although many species have a papillate lower epidermis. *Phyllanthus acuminatus* is exceptional in having definitely scabrid leaf-surfaces.

* Continued from volume XXXVII, page 122.

Rothdauscher (1896: 8) regarded the monotony of anatomical features of the leaf as virtually a tribal character of the Phyllantheae. However, while it is doubtless true that a greater diversity exists in other tribes such as the Crotoneae, the various histological characters within *Phyllanthus* provide data of considerable classificatory and evolutionary interest. Froembling (1896) indeed concurred with Rothdauscher in remarking on the great uniformity of leaf stucture in the subtribe "Euphyllantheae". But although he studied over sixty species of *Phyllanthus* (s. str.) he did not investigate a single species of sects. *Elutanthos, Williamia, Orbicularia,* or *Epistylium*, which together make up the great majority of the woody West Indian species. It is not surprising, therefore, that his observations require some modifications on the basis of various features of the species in those groups. In the following account the remarks apply particularly to the West Indian species, although they often are relevant for the entire genus as well.

In the woody species of *Phyllanthus* the upper epidermis, overlaid by a cuticle which may attain considerable thickness, is made up of more or less vertically elongated cells with outer tangential walls that are polygonal in outline. The cells of the lower epidermis are usually much smaller in surface area, inclined to be more undulate in outline (or at least less sharply polygonal), and are tangentially elongated. In the herbaceous species with thin leaves, however, the cells of the upper epidermis are not sharply polygonal in outline, and in some species the perimeter of both upper and lower epidermal cells is undulate.

Froembling (1896: 69) was content to characterize the stomata of *Phyllanthus* as extremely variable with regard to the number of subsidiary cells. However, in the leaves of the woody species the stomata are clearly the "rubiaceous" type as defined by Metcalfe and Chalk (1950: xv); there are either two — or apparently by one redivision — three subsidiary cells with their long axes parallel to the opening between the guard cells (PLATE-FIG. 18). But in leaves of herbaceous species this arrangement may become obscured due to the more irregular cell outlines. Often the guard cells are surrounded by three subsidiary cells, two parallel to the long axis of the stoma and one more or less perpendicular; such a stoma might be considered to belong to the "cruciferous" type (PLATE-FIGS. 19 & 20). In some herbaceous species such as *P. polygonoides* the arrangement is still more obscure because here there may be a number of subsidiary cells which scarcely differ in outline from the rest of the epidermal cells, and in this case the stoma would have to be classified as "ranunculaceous". Or, in the case of a number of species such as *P. niruri* there may be more than one type on the same leaf (PLATE-FIG. 21). The herbaceous species often show a significant difference in distribution of the stomata, as they often have them on both surfaces of the leaf, whereas in the woody species they are always confined to the lower epidermis. Taking the genus as a whole, there is no doubt that the basic stomatal type is the "rubiaceous", which Rothdauscher observed to be the prevailing type in the other genera of Phyllantheae.

The mesophyll in those species of *Phyllanthus* investigated thus far is composed of typical palisade and spongy parenchyma of "bifacial" leaves. The three species of "Phyllanthus" in which a foliar hypoderm was reported by Froembling (1896: 69) prove to belong to other genera. Among the West Indian species of *Phyllanthus* a definite hypoderm has been observed only in *P. myriophyllus*, although it perhaps may be discovered in other species. The palisade tissue is usually made up of a single layer of very slender cells; in coriaceous leaves with a large volume it is the spongy rather than the palisade parenchyma which is increased in bulk. Froembling reported unusual palisade cells only in the species of the Old World section *Eriococcus*. In *P. elegans* (the only species of the section which has been introduced in the West Indies) Froembling found that the portion of the cell bordering the epidermis is enlarged so that the entire cell has a clavate shape; and in *P. roxburghii* this enlarged portion is lobed so as to have the outline of a mitten. No such unusual palisade cells have been detected in any of the native West Indian species. The spongy mesophyll in the leaf of *Phyllanthus* is composed of parenchyma cells which may be arranged compactly to loosely; in some of the species of sect. *Hemiphyllanthus* the spongy layer has a striking areolate appearance due to the regular organization of the cells around circular lacunae.

Froembling reported that the veins in the *Phyllanthus* leaf are all of the embedded type, as opposed to the veins of other Phyllantheae which Rothdauscher designated as "durchgehende"; in the latter the sclerenchyma or collenchyma associated with a vein is expanded into wings which abut on the upper and lower epidermis ("vertically transcurrent" veins of Metcalfe and Chalk, 1950; xvi). During the present study of the West Indian species of *Phyllanthus*, however, both types were observed. In *P. discolor* (sect. *Williamia*) there are vertically transcurrent veins with bundle sheath extensions (Esau, 1953: 430) of collenchyma cells interrupting the palisade layer and reaching both epidermises. But within the single sect. *Orbicularia* both types have been observed. *Phyllanthus orbicularis* has rigidly coriaceous leaves with conspicuous sclerenchymatous bundle sheath extensions which tend to become uniseriate above and multiseriate beneath, as in *P. discolor*. But in the related *P. scopulorum*, which has flexibly coriaceous leaves, the veins — though armed with sclerenchyma — are clearly embedded (PLATE-FIG. 22). Some of the species with coriaceous leaves in other West Indian sections (e.g., *Thamnocharis*) resemble *P. scopulorum* in having embedded veins with massive sclerenchymatous but extensionless sheaths. In these species the rigidity of the leaf-blade is enhanced by the very massive bundle of fibers which is associated with the marginal vein and which is responsible for the prominent rim-like margin of the leaf (PLATE-FIG. 23).

The veins of the *Phyllanthus* leaf are pinnately branched, and the laterals ordinarily ramify considerably and then unite near the margin to produce an arcuate marginal vein. The foliar vascular systems of individual species differ widely from one another in such details as branching pattern, massiveness, development of parenchyma vs. sclerenchyma in

bundle sheaths, and vein endings; consequently, despite the great variation in some of these characters, leaf vascular tissue appears to be a promising source of systematically valuable criteria. In species with membranous or chartaceous leaves, only the midrib and larger veins are jacketed with sclerenchyma; and the ultimate veinlet tips lying free in the mesophyll are bordered (if at all) only by parenchyma sheath cells. The veins of many species end with one or two essentially unmodified tracheids (PLATE-FIGS. 28, 30); but in other species one or more of the terminal tracheids are modified into swollen "storage tracheids" ("Speichertracheiden"; PLATE-FIG. 29). In some species with coriaceous leaves, however, the fibers of the bundle sheath extend out even to the ends of the minor veins; and in several species, such as *P. microdictyus*, the sclerenchymatous elements flare beyond the tips of the last tracheid (PLATE-FIG. 24).

The designation of these sclerenchymatous elements presents a rather difficult problem in terminology. In the following discussion these elements which project into the mesophyllar spaces of the leaf will be called "foliar sclereids", following the usage of Foster (1946). The sclereids of *Phyllanthus* would mostly belong to either Type III or Type IV of Foster's classification, for they are always elongated and not highly branched. In fact, except for their position and occasional branching the sclereids of *Phyllanthus* could just as well be called fibers. However, in a few species (e.g., *P. chryseus* and *P. comptus*) the sclerification of the veinlet-ends is due to peculiar, sometimes deformed, sclerenchymatous elements which are more or less intermediate between sclereids and tracheids (PLATE-FIG. 31).

Within the evolutionary series formed by the three related sections *Williamia*, *Williamiandra*, and *Orbicularia*, a trend of increasing sclerification is strikingly apparent. In the most primitive species of the complex, *P. discolor*, the ultimate veinlets are naked. The other species of sect. *Williamia*, *P. microdictyus*, exhibits sclereids which project beyond the veinlet-tips, as mentioned above. In sects. *Williamiandra* and *Orbicularia* the exsertion of the sclereids has become far more pronounced, and the massive veins and free-lying portions of the sclereids occupy a very appreciable portion of the volume of the leaf (PLATE-FIGS. 25–27). In sect. *Williamiandra* (and sometimes in *Orbicularia*) many of these elongated sclereids extend vertically through the leaf as columns which abut against the upper and lower epidermis in the manner of the Type III sclereids illustrated by Foster for *Mouriri pusa* (1946: fig. 16). It is furthermore very interesting that sclereids of this kind have arisen independently in *P. duidae*, a species of the unrelated South American sect. *Microglochidion*.

On the basis of the observations made so far it can be said that the foliar sclereids of *Phyllanthus* appear to be terminal in origin and to have been derived from the fiber-like sclerenchymatous cells of the bundle sheath. Diffuse sclereids or stone cells have not been observed in the leaf of any species of *Phyllanthus*. Furthermore, foliar sclereids have thus far been detected only in the New World species. However, since they have originated independently in the West Indian and South American species,

there is no reason why they could not occur in some of the Old World species; further investigation of the leaves of the latter is therefore desirable.

As Froembling reported, almost all species of *Phyllanthus* which have been examined prove to have crystals, most often druses, in the mesophyll. In a smaller but still considerable number of species rhombic or prismatic crystals are produced as well. There is a definite tendency for the druses to occur in the layers of cells directly adjacent to the upper and lower epidermis, but occasional ones may also be found scattered in the mesophyll, and both druses and rhombic crystals may occur along the veins. The use of crystals as a taxonomic character is attended with the disadvantage that their expression may vary within a single species and that they may change form in cleared mounts which have been treated with caustic soda, as reported by Heintzelman and Howard (1948). It appears doubtful that the study of crystals will afford much assistance in distinguishing closely related species; but it is possible that a sufficiently broad survey might provide useful evidence on the supraspecific level. For example, the species of sect. *Orbicularia* appear to differ from most of the related sections such as *Williamia*, *Epistylium*, and *Thamnocharis* in having both rhombic crystals and druses, while the latter have druses alone.

Petiole.

The petiole of all species of *Phyllanthus* is quite short and never approaches the length of the blade. Ordinarily it has an uncomplicated form, being plane adaxially and more or less convex abaxially, sometimes with a flange of green tissue decurrent from the blade. In sect. *Asterandra* this flange is very distinctively modified by transverse pleating into an accordion-like shape, so that isolated leaves of this group are always easy to identify.

Anatomically, the structure of the petiole conforms to the simplicity of the external form. The epidermis consists of small squarish cells, and stomata have not been observed. The vascular tissue as seen in cross-section (PLATE-FIG. 5) assumes the form of a slightly adaxially concave arc, with no conspicuous wings, flanges, or exclaves of vascular tissue such as have been reported in the petioles of many Euphorbiaceae (Dehay, 1935). In *P. urinaria*, however, the usual situation is modified by the presence of a curious reticulum of many fine inter-connected tracheids which form a mesh on all sides of the central vascular core. This accessory tracheary tissue is probably correlated with the pulvinar nature of the petiole; the leaves of *P. urinaria* have been reported to be "sensitive" to touch.

Crystals are usually more abundant in the petiole than in the blade, and the proportion of druses to rhombic crystals may be different. Sclerenchyma often forms a conspicuous jacket around the vascular tissue, but no free sclereids or stone cells have been observed.

Stipules.

The leaves of *Phyllanthus* are always stipulate, although in some species the stipules are evanescent and thus at first sight may appear to be absent. Most commonly the stipules are triangular to lanceolate with an acute or acuminate, sometimes reflexed, tip. The margins and tip are usually scarious at maturity and are differently colored from the herbaceous basal area. The scarious portion of the stipule is composed of tabular cells without stomata and is often denticulate at the margin. The basal herbaceous portion, which may have stomata, is often thickened and persistent after the fall of the scarious tip.

Although the stipules of *Phyllanthus* never become as large and foliaceous as in species of *Amanoa* or *Drypetes*, they do show extensive variations in duration, size, shape, color, development of auricles, marginal toothing, etc. For this reason they provide some of the most convenient characters for readily distinguishing species. Measuring the sizes of stipules has the slight inconvenience that those of the proximal portion of branch or branchlet are usually larger than the distal ones; and the two at the same axil may be unequal. In *P. formosus* the two members of each stipule-pair are extraordinarily unlike, one of them being broad and conspicuously lacerate-dentate while the other is narrow and quite entire. This approaches the extreme heteromorphy of the stipules in *Vicia monantha* as illustrated by Glück (1919: fig. 2).

The species other than *P. formosus* do not have such a dimorphism of stipules on the same branchlet. However, in most species with phyllanthoid branching the stipules on the deciduous branchlet are quite different from those on the permanent axis; the latter are usually larger, broader, and of a much firmer texture. In many woody species these permanent-branch stipules are clustered at the apex of the stem into a dense scaly cone which encloses the apical meristem and unexpanded leafy branchlets. In such woody species as *P. cinctus* these stipules are indurate and the numerous parallel veins are stoutly armed with sclereids. In most herbaceous and some woody species of *Phyllanthus* the stipules have only a single vein which is not jacketed with sclereids (PLATE-FIG. 5).

Cataphylls.

In the section on growth form one of the essential characters of phyllanthoid branching was shown to be the reduction of the leaves on the seedling stem (and all subsequent persistent axes) to cataphylls, the reduced leaf blade usually resembling the stipules in appearance and thus three stipules appearing to be at the same axil. Actually, although the reduced blade of the cataphyll is usually just like the stipules in texture and color, it is very often narrower and thus may be distinguished by its shape and position.

The spatial relationship of the cataphylls in *Phyllanthus* is rather peculiar. They do not correspond to conventional cataphylls as defined, for instance, by Gray (1879: 401) or Goebel (1905: 384). As Goebel pointed

out, the term was originally coined by Schimper to refer to the scale leaves on rhizomes or the basal parts of aerial stems. Goebel added:

> "To these leaf formations, both in their construction and function, all those epigeous parts which have been called bud scales (tegmenta) conform, and so closely that they have received the same name. This is not altogether wrong, inasmuch as these leaf formations upon an upright growing shoot stand upon the "lower" region of the shoot and are followed by foliage leaves."

The cataphylls of *Phyllanthus*, however, do not correspond either to rhizome scales or bud scales, for they definitely appear on the upper portions of stems and branches and are *preceded* by typical leaves. Their position on the axis therefore appears to be the reverse of that of typical cataphylls. Jackson (1905: 131), would have called the scale-leaf of *Phyllanthus* a "hypsophyll", which is defined by him as "a bract of the inflorescence, a reduced or modified leaf towards the upper end of the shoot." As Goebel (1905: 390–391) remarked, however, it appears best to retain the word "hypsophyll" for those leaves directly associated with flowers. In form and evidently in function the scale-leaves of *Phyllanthus* resemble typical cataphylls, and their different position does not appear to be of fundamental importance. The main difference between the cataphylls of *Phyllanthus* and most bud-scales is that the latter are associated with seasonal growth.

Majumdar and Arshad Ali (1956) have studied the vascular anatomy of the cataphylls in *Phyllanthus amarus* (*"niruri"*) and *P. reticulatus*. They report that in *P. reticulatus* (which has trilacunar nodes) the traces from the lateral leaf-gaps of the node run into the stipules; the median trace gives off two branches which turn back and join the stipular traces. This observation has been personally verified as far as the branchlet of *P. reticulatus* is concerned. In *P. amarus*, on the other hand, they report that the main axis has unilacunar nodes (although the nodes of the deciduous branchlet are trilacunar) and that the two lateral branches of the median trace (midrib) pass directly into the stipules. Because of this difference they call the appendages of the *P. amarus* cataphyll "leaf lobes" and those of *P. reticulatus* "stipules"; but then they qualify this by adding that the difference between basal lobes and stipules in this case "is one of degree [rather] than of kind". It is difficult as yet to evaluate these very interesting observations on the basis of the nodal anatomy of only two species of a genus as large as *Phyllanthus*. Despite the behavior of the traces, there is no difference in the cataphyllar stipules of *P. amarus* and *P. reticulatus* which would warrant giving them different names. Furthermore, the fact that the leaf-blade of *Phyllanthus* is always simple and entire quite precludes the possibility of *P. amarus* having three-lobed leaves. What the researches of Majumdar and Arshad Ali do show is that, as might be expected, the foliar traces of the advanced herbaceous species *P. amarus* have undergone considerable modification and reduction as compared to the more primitive *P. reticulatus*.

Anatomically the blade of the cataphyll in *Phyllanthus* is completely

different from the foliage leaf and closely resembles the accompanying two stipules. Stomata, palisade cells, and spongy parenchyma are lacking (at least in the expanded scarious portion), the epidermal cells are tabular and thick-walled, and the veins (if more than one) are parallel. In some of the herbaceous species of sect. *Phyllanthus* transitional forms between foliage leaf and cataphyll occur, particularly at the proximal nodes of permanent branches. These have a green foliose proximal part which distally is abruptly contracted into a brownish scarious tip. The cataphyll of some of the species of sect. *Orbicularia* (e.g., *P. scopulorum*) is especially interesting because the blade closely resembles the long scarious deciduous tip of the foliage leaf. This suggests that in some species of *Phyllanthus*, at least, the cataphylls would belong to the category of those derived mainly from leaf apex (cf. Schulze, 1934). However, drawing a strict homology between leaf apex and cataphyll blade would scarcely be justified until comparative developmental studies have been made.

Dingler (1885: 139) found in studying the seedling of *P. niruri* that the reduction of the foliage leaf to cataphyll occurs at the node where the first deciduous branchlet is attached; he therefore concluded that there is a direct causal relationship at work. It might be supposed, consequently, that it is the precocious expansion of the branchlet which inhibits the lamina of the cataphyll. However, the correlation between reduction of cataphyll blade and development of deciduous branchlet does not appear to be as exact as Dingler suggested. Examination of seedlings of *P. abnormis*, *P. amarus*, and *P. tenellus* has shown that the abrupt change from foliage leaf to cataphyll by no means takes place at precisely the same node where the first deciduous branchlet appears. Furthermore, there are a number of species (e.g., *P. formosus*, *P. berteroanus*, and *P. sellowianus*) with undoubted phyllanthoid branching in which the reduction of foliage leaf to cataphyll takes place considerably later in ontogeny or not at all. Nevertheless, there is in a general way an undoubted inverse correlation between development of deciduous branchlets and the blades of the leaves on the permanent axes.

Trichomes.

The great majority of the species of *Phyllanthus* may be described as completely glabrous, but many of them have a papillate lower epidermis, and in a few species papillae may occur on the upper leaf-surface as well. As Froembling pointed out, there are some species (e.g., *P. praetervisus*) in which all manner of transitions may be observed between epidermal cells which have merely a convex outer wall to those in which the cell is drawn out into a long hair. The hairs are uniseriate, composed of one to several cells, thin-walled, and usually obtuse at the ends. Foliar glands or capitate hairs of the sort found in the Crotoneae are unknown in the Phyllanthinae. Froembling's report that unicellular hairs of *Phyllanthus* often assume a nearly uncinate form probably applies to species now included in *Glochidion*; in both genera, however, the hairs are never as long, sharp-pointed, and pronouncedly uncinate as those in the Andrachninae.

Among the native West Indies species well-developed trichomes occur in only a few groups. In sect. *Elutanthos* multicellular hairs occur on both stem and leaf, but their expression is quite variable, and *P. botryanthus* is completely glabrous. In sect. *Hemiphyllanthus* trichomes occur only on the axes, where they are clustered on peculiar longitudinal plates or ridges of cells. The result is an incrustate appearance which recalls that of the twigs in sect. *Williamiandra*, which have incrustate masses of cells that are derived from proliferation of lenticellar tissue.

INFLORESCENCE

The best general treatment of the inflorescence of the Euphorbiaceae (excluding the Euphorbiae!), despite its age, is that of Baillon (1858). He clearly stated that the cymose pattern is the most widespread and fundamental both in the Euphorbiaceae and the angiosperms as a whole. The study of the inflorescence of *Phyllanthus* agrees well with this and with the hypothesis of Rickett (1944) that the *dichasium*, or "complete cyme" of Gray (1879) is the basic type of which all other angiospermous inflorescences represent modifications. In many Euphorbiaceae the flower arrangement has become so highly modified that its fundamentally cymose nature is apparent only on careful inspection. In *Phyllanthus*, however, there is little doubt except for those few species with solitary flowers; and there is furthermore a broad spectrum of inflorescence types which can be related to one another.

The individual cyme in *Phyllanthus* is of course a determinate structure with a terminal female flower (if it is bisexual). But in those species with cymes aggregated into a compound inflorescence, the latter is indeterminate; there is never a single flower terminating the main axis as in *Jatropha* or *Euphorbia*. Since it appears that the phylogenetic trend of inflorescence modification in *Phyllanthus* has been one of reduction, the more elaborate types will be considered first.

The species of sect. *Elutanthos* have the least modified kind of inflorescence among the West Indian species and — except for the Australasian sect. *Nymania* — the genus as a whole. Of the species of sect. *Elutanthos* the Mexican *P. grandifolius* has the most elaborate aggregations of flowers. The proximal portion of the floriferous branch (i.e., the branch of the current year) bears normal foliage leaves, some of which subtend thyrses of male flowers. Each male thyrse is composed of a number of cymules arranged alternately on the flexuous axis. The male cymules are dichasial only at the very base and monochasial thereafter, so that two or three "pseudo-racemes" of flowers appear fascicled together at one node. The distal portion of the floriferous branch is itself modified into a thyrse which only differs from the male inflorescence in that the individual cymules have fewer flowers and thus are more fascicle-like than raceme-like.

Phyllanthus grandifolius is interesting not only because of its elaborate aggregations of flowers, but also because it shows in an unspecialized condition the tendencies which lead toward the inflorescences of other

species. For example, two trends ocurring in *P. grandifolius* and in many other species are: monochasial development of cymules and production of male flowers proximally relative to the female flowers (on the entire branchlet or thyrse). In *P. grandifolius* the sexes are more or less completely segregated, the male flowers being borne on axes in the axils of normal foliage leaves and the female directly in the axils of the distal leaves, which are usually reduced to bracts. There is thus in this species a striking (though not invariable) correlation between the terminalization of the female flowers and the reduction of the subtending leaves to bracts. This reduction phenomenon may not be taken as a general rule, however, because in other species it is the proximal leaves subtending the male flowers which are reduced. The terminalization of the female flowers, on the other hand, occurs almost invariably whenever the plant is monoecious and the cymules unisexual; only in the few species of sect. *Urinaria* is the order definitely reverse.

The West Indian species of sect. *Elutanthos* differ from *P. grandifolius* in having mostly bisexual cymules and less elaborate inflorescences. The flower arrangement in these, and all the other species with non-phyllanthoid branching, is so variable and dependent on the vigor of the shoot that it is very difficult to write a good taxonomic description of it. In *P. nutans*, for example, the female flowers tend to be clustered in the axils of reduced leaves on a flexuous "semi-naked" axis (more exactly, a racemiform thyrse), while the male flowers are borne either in clusters axillary to foliage leaves or at the lower nodes of the thyrse. In this, as in all the species of sect. *Elutanthos*, the boundary between the vegetative and fertile zones of the plant is not well defined.

In the herbaceous or subshrubby species of sect. *Paraphyllanthus*, (none of which occur in the West Indies), the cymules are reduced to dense clusters that are always axillary to foliage leaves. The flower-clusters are extremely variable, at least in the widespread *P. polygonoides*, which may be either monoecious or dioecious and which may have both unisexual and bisexual cymules on the same individual. Furthermore, branch buds may be produced at the same axil as a flower cluster.

The three West Indian species of sect. *Loxopodium* have a similar sort of floral arrangement, and branch-buds may similarly be produced at the same axils with the flowers; but usually the arrangement of the sexes is much more definite as to number and position. The cymules may contain from one to five female flowers and as many male, but the inflorescence axis is always so greatly contracted that it is not evident to casual inspection. There thus appears to be no fundamental difference between the pattern of flower production in the various sections with non-phyllanthoid branching; flowers may be produced (at least potentially) at any node on any axis (except possibly for the lowermost nodes on the seedling axis).

In the remainder of the West Indian species, however, as well as in the majority of those in the entire genus, the flowers are borne only on deciduous branchlets and never on the main axis or on permanent branches. Among these West Indian species with phyllanthoid branching, *P. juglandi-*

folius displays relatively unspecialized inflorescences. The cymules are mostly bisexual, and those of the proximal axils of a branchlet often have three or four female flowers accompanied by several males; the number of female flowers decreases distally until the cymules at the tip of the branchlet are entirely male. In a few other species such as *P. discolor* there may be two or three female flowers per cymule, but in most species there is only a single female flower and the cymules are often unisexual. *Phyllanthus juglandifolius* is exceptional not only in its relatively elaborate inflorescences, but more especially in its tendency toward proximal production of female flowers, which is exactly the reverse of the trend in most other species.

Perhaps the most striking evolutionary trend is apparent among the herbaceous species with phyllanthoid branching, in which there is a very evident shift from bisexual to unisexual inflorescences. With the exception of the anomalous *P. elsiae* there are no woody American species of *Phyllanthus* which are dioecious; but in a number of the herbaceous species of sect. *Phyllanthus* entire plants, as well as individual cymules, may be unisexual. However, even in these species the dioecious condition is not absolute, for male branchlets will occasionally produce one or two female flowers at the tip, and while female branchlets never produce any male flowers (at least in the West Indian species) a female plant may produce a few male branchlets. In contrast to this imperfect dioeciousness in *Phyllanthus*, the West Indian representatives of the related genera *Astrocasia, Flueggea, Savia,* and *Securinega* appear to be completely dioecious.

In most of the herbaceous species of sect. *Phyllanthus* the combination of the trends toward unisexuality of cymule and terminalization of female flower has resulted in branchlets with proximal cymules of several male flowers and distal cymules each of a solitary female flower. The common weedy species *P. amarus* is exceptional in that it has bisexual cymules, each with one male and one female flower.

In a few species the reduction of the cymule has proceeded to the point where it is composed only of a solitary flower. This situation prevails in the herbaceous species of sects. *Callitrichoides* and *Cyclanthera* and in several shrubby species of sect. *Orbicularia*. Among the latter, however, the condition is not as strongly fixed, for occasionally paired flowers may be produced on a branchlet which otherwise has only solitary ones.

The West Indian species with bipinnatiform branchlets have a special sort of distribution of flowers. In *P. subglomeratus* and many of the South American representatives of sect. *Nothoclema* cymules are produced at all the nodes of both the ultimate and penultimate axes. In the other West Indian species of *Nothoclema*, *P. acuminatus*, flowers are likewise produced at all the nodes of the ultimate axes; but on the penultimate axis there are cymules only at the proximal nodes which do not subtend ultimate axes, and sometimes there are no floriferous nodes on the penultimate axis. In the species of sect. *Hemiphyllanthus* this "sterilization" is complete and flowers are produced only on the ultimate axes.

In the section on growth form the origin of cauliflory in *Phyllanthus* has been ascribed to the modification of floriferous branchlets to "naked" thyrses with the leaves reduced to scales and to the production of these modified branchlets in fascicles at nodes of the previous year's growth. It is probable that among the species represented in the West Indies, cauliflory has arisen independently at least twice: in sect. *Cicca* and in sect. *Epistylium*. The basic prerequisite for cauliflory is of course the reduction of the leaves subtending the cymules; but in *Phyllanthus* there is evidently not a very strong trend in that direction. It is true that in a great many species the proximal leaves of a branchlet are often smaller than the distal ones and subtend male cymules; this suggests that there may be some nutritional effect on both the expression of leaf size and sex of flowers. But on the other hand there are a number of species in which the correlation is reversed and it is the distal leaves subtending the female cymules which are reduced. This diversity in sex expression and leaf modification raises some interesting physiological problems. The species with phyllanthoid branching would seem to be promising experimental plants for research in sex determination such as that carried out by Nitsch et al. (1952) on the Cucurbitaceae. These authors showed that sex expression in the cucumber may be controlled by varying temperature and light, at least to the extent of modifying the number of nodes bearing a particular kind of flower. Similar experiments carried out with the view of comparing the response of a species of sect. *Urinaria* (with female flowers proximal on the branchlet) and a species of sect. *Phyllanthus* (with the female flowers distal) might yield significant results.

Croizat (1943, 1944) has discussed the morphology and evolution of inflorescence in *Phyllanthus* and has suggested a different interpretation from that adopted here. In his first paper he asserted:

> "In certain groups of *Phyllanthus* true leaves are present, the florigerous axes being often reduced, bracteate, and, strictly speaking, leafless branchlets (see *P. laxiflorus* [*P. grandifolius*]). In other groups of the same genus the true leaves are represented only by scales, the aspect and function of foliage being assumed by the bracts of the florigerous axes (see *P. mexiae*)."

In his fuller account the following year it is evident that Croizat's view of the evolution of inflorescence in *Phyllanthus* is based on two main assumptions: first, that the solitary axillary flower represents the primitive type of inflorescence, and second, that the foliage leaves of species with phyllanthoid branching represent bracts which have presumably been "de-differentiated" into leaves. Majumdar and Arshad Ali (1956: 158), on the basis of their studies of *P. amarus* and *P. reticulatus*, have come to a similar conclusion as regards the latter point. Because the buds in the axils of the leaves of the branchlet produce only flowers, they suggest that the branchlets of these two species should be called inflorescences and the leaves should be called bracts.

The term *anthocladium* has been applied by Goebel (1931) to a branch in which the determinate (i.e. cymose) branching pattern of the inflores-

cence is superimposed on the indeterminate pattern of the vegetative shoot. In *Phyllanthus*, as specifically pointed out by Goebel (1931: 22), the floriferous axis is monopodial and thus cannot strictly be termed an anthocladium. Nevertheless, it is very evident that in *Phyllanthus* the fate of the deciduous branchlet is intimately related to flower production.* But to call either the anthocladium of *Euphorbia* subg. *Chamaesyce* or the deciduous branchlet of *Phyllanthus* an "inflorescence" is not only unwarranted but holds the danger of introducing confusion in terms. In all the species of *Phyllanthus* investigated, the leaves subtending the cymules are typical foliage leaves indistinguishable (except sometimes by a minor difference in shape) from those on the seedling axis. If one were to follow Croizat and Majumdar in calling the branchlet leaves "bracts", this would contradict the classical definition of the latter term (cf. Gray, 1879: 118), which definitely requires a bract to show a difference in form. Furthermore, neither in *Phyllanthus* nor in *Euphorbia* subg. *Chamaesyce* is there any evidence that the leaves associated with the flowers or cyathia have metamorphosed back from bracts.

FLOWER

Few other genera of angiosperms display a range of variation in flower structure comparable to *Phyllanthus*, even when such divergent groups as *Astrocasia* and *Margaritaria* have been removed from it. It is not surprising, therefore, that during the first half of the nineteenth century many small genera justified by "technical" floral characters were erected on various species now included in *Phyllanthus*. One of Mueller's greatest accomplishments was his perception of the essential similarity between these many small "genera", and his synthesis of these fragments into a unified and — on the whole — natural generic concept. In placing *Glochidion* within the confines of *Phyllanthus*, Mueller emphasized the relationship of these two groups in floral morphology, and Hooker implicitly recognized this when he had to justify the resurrection of *Glochidion* chiefly on the grounds of convenience.

Floral diversity is enhanced in *Phyllanthus*, as in other genera of the Euphorbiaceae, by virtue of the fact that the male and female flowers have often evolved in different ways. But at the same time there has been in both sexes a trend towards reduction of number of parts, accompanied by a decrease in variability. The structural differences between the male and female flowers in the various species may be ascribed to the interaction of two factors: the duration of the flower (the male being relatively fugacious) and the difference in the number of sporophylls. It appears that in some instances the number of calyx-lobes developed in the mature flower is affected by the shape of the androecium or gynoecium primordium during development. Thus in an appreciable number of the species which

* From a dynamic point of view it might be worth while to broaden the definition of "anthocladium" to include highly specialized monopodial branches which behave as inflorescence-units.

have male flowers with only two stamens the calyx-lobes of the male flower are reduced from five to four, whereas the female flowers still have five calyx-lobes.

The flowers of *Phyllanthus* are exclusively unisexual, and ordinarily there is no trace of the organs of the missing sex. Section *Cicca* is the only group in which definite staminodes occur; and these may even produce a few pollen grains, though it is not known if any of these "female" pollen grains are fertile. From time to time various authors have described species of *Phyllanthus* with a "pistillode" in the male flower, but on close examination this structure has always proved to be the apiculate tip of the staminal column, which may represent either an abortive stamen or one or more prolonged anther connectives. Any "Phyllanthus-like" plant which does have a pistillode may confidently be referred to some other genus.

The floral biology of *Phyllanthus* remains an almost uncharted area, partly because so many of the species grow in localities where protracted field observation is difficult. The great diversity in flower structure suggests specialization for different types of insect visitors, but almost nothing is known of how any of the species are pollinated. Personal observation in Cuba of the pollination of *P. dimorphus* by chrysomelid beetles (unfortunately not further identified) and of *P. orbicularis* by bees has given the merest glimpse into the pollination relationships of the genus.

Pedicel and Torus.

The pedicel of the male flower is terete, usually slender, and is about as long as or longer than that of the female flower. This proves to be a good, albeit superficial, character for distinguishing *Phyllanthus* from related genera such as *Savia* and *Securinega*, where the male flowers are mostly subsessile and the female flowers long-stalked. In a few species of *Phyllanthus* (e.g., *P. tenellus*) the pedicel of the female flower is much longer that that of the male, but usually it is shorter and in some species such as *P. urinaria* is shortened to scarcely more than a broad platform beneath the calyx.

Histologically, the pedicel is usually rather simple. The epidermis (in the proximal portion, at least) lacks stomata and is composed of cells with rectangular outlines. A "hypodermis" may sometimes be distinguished, at least in the base of the pedicel, by the tannin content of the subepidermal layer. In all of the male flowers examined, sclereids are completely absent, the axis of the pedicel being occupied only by a few slender tracheids. The female flowers of many species likewise have only tracheids, but the pedicel of *P. niruri* shows a very characteristic sclerification. Towards the base of the pedicel slightly elongated "brachysclereids" occur around the outside of the vascular bundle; these become progressively longer distally but stop about halfway up the pedicel. Beneath the brachysclereid layer, however, is a layer of fibers which run to the very top of the pedicel

and end in the receptacular region. It is very curious that some of the woody species examined, although having much larger fruit than *P. niruri*, entirely lack fibers or sclereids in the pedicel. Crystals are typically much less numerous in the pedicel proper than in the receptacle or ovary.

The top (distal) portion of the pedicel is expanded (sometimes abruptly) into a receptacle which merges with the basally fused calyx lobes so that it is neither conspicuous nor clearly defined. In the female flower the upper portion of the pedicel may gradually (as compared with the male) enlarge up to the toral region, and in some of the species of sect. *Hemiphyllanthus* this dilated portion may become large and fleshy. The enlargement reaches such grotesque proportions in the female flower of *P. megapodus* that the expanded pedicel-receptacle is larger than the rest of the flower. In *P. subcarnosus* the expanded portion of the pedicel contains chlorenchyma.

The pedicel characteristically hangs so that the male and female flowers project below the plane of the leaves on the branchlet. After the fertilization period the pedicel of the male flower disarticulates, but that of the female flower remains relatively unchanged. During the development of the fruit the pedicel may elongate slightly, but (at least in the West Indian species) the increase in length is never very great.

Calyx.

The flowers of *Phyllanthus*, in common with those of most of the Euphorbiaceae, are apetalous with a gamophyllous calyx. The union of the calyx-lobes at the base is sometimes slight but almost always noticeable on close inspection, and except in very rare instances (e.g., *P. subcarnosus*) they never disarticulate separately from the receptacle. In many species the calyx, as if in compensation for the lack of petals, is petalloid and conspicuous, red or pink (and more rarely purplish) being the prevailing hues; and the disk is often of a contrasting color. In other species, particularly the herbaceous ones, the calyx is yellowish or whitish, and in a few the female calyx is green and foliose.

As suggested by Michaelis (1924) for the Euphorbiaceae as a whole, the basic arrangement of the calyx-parts in *Phyllanthus* appears to be five lobes in imbricate aestivation; four lobes in decussate pairs or six in two whorls represent derived conditions. The number of lobes may vary within the same species, and does not necessarily correspond between the male and female flowers. Although the male and female calyces of some species are very similar, the female calyx is very often larger, stouter, and composed of a greater number of lobes.

Usually each calyx-lobe of the male flower has a single unbranched or sparsely branched vein; in the latter case, the branch-tips, of more or less enlarged tracheids, occur flabellately near the tip of the lobe. In species with fairly massive male flowers, such as those of sect. *Thamnocharis*, there may be three parallel sparsely branching veins. The calyx of the female flower usually has more elaborate venation than that of

the male. In sect. *Paraphyllanthus* (which is not represented in the West Indies) the female calyx-lobes are quite green and foliaceous; the mid-vein branches much as in the leaf to form a reticulate pattern, and the interior of the lobe is occupied by chlorenchyma. The calyx-lobes of the species in this section are more leaf-like than those of any of the West Indian species, which have no well-defined chlorenchyma. However, stomata occur on the epidermis of the female flowers of many species and rarely even on the epidermis of the male (e.g., *P. ekmanii*). Reticulate venation is not well-developed in the calyx-lobes of any of the West Indian species, but in the lobes of species with massive female flowers (such as in sect. *Thamnocharis*) there are instead a number of parallel veins conspicuously jacketed with fibers.

The texture of the calyx varies from thinly herbaceous to coriaceous among different species; the margins even of the coriaceous lobes are thin, and sometimes are denticulate or lacerate. At anthesis the calyx-lobes of both male and female flowers are usually more or less spreading, but in some species the lobes of the female calyx remain erect and imbricate around the ovary. The female calyx remains relatively unchanged during maturation of the fruit except that sometimes the lobes become reflexed. *Phyllanthus subcarnosus* (sect. *Omphacodes*) is exceptional in that the female calyx-lobes are very early deciduous from the receptacle.

Disk.

The term *disk* as used here refers to the more or less glandular mass of tissue arising from the receptacle between the calyx and the androecium or gynoecium. In *Phyllanthus* the disk is invariably outside the stamens; but the situation is reversed in some other genera of Phyllantheae such as *Drypetes* and *Reverchonia*. In the male flower the disk is ordinarily divided into segments isomerous and alternating with the calyx-lobes. The disk-segments are often closely contiguous and they may be united in pairs or all united into a continuous saucer- or cup-shaded disk. A few species such as *P. emblica* have male flowers with the disk reduced or absent, and in *P. elsiae* the disk is absent in both sexes; the latter situation prevails in other genera of the Phyllanthinae such as *Glochidion* and *Breynia*. In the female flower of *Phyllanthus* the disk is most commonly continuous, and only in a rather small number of species is it divided into segments like the disk in the male flower.

The term *disk-segment* as used here is synonymous with the "disk-gland" of most authors. The latter term is unwieldy because there are some species of *Phyllanthus* in which the disk-segment is itself provided with glands. The disk-segment is more or less equivalent to the "nectary," but the latter term suffers from the ambiguity that it is sometimes applied to the entire disk of a flower and sometimes to the individual disk-segments. It must be kept in mind that the disk-segment is a topographical designation and is not intended to convey any developmental implications. The disk does not necessarily begin development as an entire structure and then break up into segments, either in ontogeny or phylogeny.

The disk may be greenish, yellowish, pink, or even deep red or purple when fresh, but on drying it usually loses its distinctive color and becomes brownish. In many species the disk-segments are crenulate or lobed and appear pitted under high magnification. Microtome sections show that in *P. reticulatus*, for instance, there is a stoma at the bottom of each of the well-like pits, and that the cells making up the disk are smaller and have denser cytoplasm than those in most of the other floral parts (PLATE-FIG. 46). Stomatal pits have been observed in the disk of most of the species studied from paraffin sections, and in some species (e.g., *P. ekmanii*) they can be easily seen in cleared whole mounts. This histological evidence leaves little doubt that the disk of *Phyllanthus* is a true nectary in function. The amount of nectar secreted by the disk is evidently small in most species, since the disk of flowers examined in the field usually appears merely moist. A considerable quantity of nectar has been observed only in *P. polygonoides*, an extra-Caribbean species. The flowers of most species appear to be quite odorless, but it has been reported that the common *P. epiphyllanthus* has flowers which give off an evil smell at night.

Many species have flowers with a relatively massive disk in one or both sexes. The Indonesian species *P. ceramanthus*,* with both the androecium and gynoecium almost completely enclosed in an urceolate disk, represents the extreme in vertical extension. *Phyllanthus emblica* has the most disparate disk structure in the two sexes of any species examined; the female disk is a cup like that of *P. ceramanthus* and with a lacerate rim, but the male is reduced or absent. The West Indian *P. chryseus* is of especial interest, not only because it has the relatively largest disk of any species examined, but also because of the vascular supply to it (PLATE-FIG. 45). In species such as *P. reticulatus*, which have a much smaller floral disk, there is no sign of a special vascular supply. This suggests that in *Phyllanthus*, at least, vascularization of the disk is a function of size and can have no particular significance for purposes of homologizing different parts of the flower.

The question of the morphological nature of the disk in the Euphorbiaceae is of some theoretical interest and has been discussed by a number of workers. Baillon (1858) clearly distinguished between staminode and disk; he regarded the latter as an expansion of the torus on the basis of his ontogenetic studies. His view is clearly shown in his discussion of the hypogynous glands of *Cluytia pulchella*:

> "Quant aux cinq glandes bilobées de la fleur femelle, elles constituent un vrai disque, et l'on peut suivre facilement . . . son developpement ulterieur a celui du pistil. Si c'etaient des staminodes, elles apparatraient avant lui."

Baillon's assumption that there is a perfect correlation between the morphological nature of floral organs and the time of their initiation in development is bound to be suspect in this sceptical age. Michaelis (1924: 113), on the basis of his own studies on the Euphorbiaceae, does not con-

* **Phyllanthus ceramanthus** nom. nov.; *Ceramanthus gracilis* Hassk. Cat. Hort. Bogor. Alt. 240. 1844; non *Phyllanthus gracilis* Roxb. Fl. Ind. 3: 655. 1832.

sider the delayed appearance of the disk a proof against its staminodial origin. He found that in *Croton* and *Codiaeum* rudimentary calyx- and corolla-parts were delayed in ontogeny, and concluded therefore that the late appearance of the disk may likewise be only an indication of its rudimentary nature. The entire problem appears to need reinvestigation; but in any event, ontogenetic studies of *Phyllanthus* — in which the disk always appears very late — do not seem likely to provide decisive evidence.

Eichler, in his "Blütendiagramme" (1875: 4, 48–49) regarded the disk in most angiosperms as representing an emergence of the axis (specifically, the receptacle). In addition to remarking on the belated development of the disk, he added the important generality that the disk structures do not alter the arrangement of whorls in the flower and therefore cannot represent an independent cycle. Bentham and Hooker (1880: 239), Pax (1890: 1) and Pax and Hoffmann (1931: 13) followed Eichler's conception in interpreting the disk in the Euphorbiaceae.

A different interpretation has been presented by Michaelis (1924), who in a vigorous refutation of the "emergence" theory has suggested that the disk-structures of the Euphorbiaceae are mostly derived from reduced stamens. His argument is based on a number of his observations: (1) the regularity of position of the "Diskusdrüsen," which occupy the positions of the outer staminal whorl; (2) the resemblance of the disk-segments of *Chiropetalum*, *Cluytia*, et al., to immature stamens; (3) the development of "archesporial tissue" in the disk-segments of *Erythrococca*; (4) the occasional replacement of "disk-glands" by stamens; and (5) the lack of appreciable nectar or sugar content in the disk.

In the present study Michaelis's viewpoint has been considered only as it relates to the Phyllantheae, and no attempt has been made to check his observations on members of the Crotonoideae. A detailed reading of his work shows that he depended heavily on evidence from the polyandrous species of *Croton*, in which the disk-segments alternate with the petals and thus occupy the position of an outer staminal whorl. However, at least in the more primitive genera of Phyllantheae the disk-segments (where separate) are definitely opposite the petals and can scarcely represent an abortive outer staminal whorl. Furthermore, in the occasional hermaphroditic flowers of *Phyllanthus acidus*, the staminodes appear in addition to the normal hypogynous disk; in this species, therefore, there can hardly be any doubt that the disk is not staminodial in origin.

It is difficult to understand Michaelis's contention that the disk does not play a rôle as a nectary. It is true that, as he asserts, there is no evident amount of free nectar in the flowers of many Euphorbiaceae. But in *Phyllanthus*, at any rate, the anatomical structure of the disk shows that there can be little doubt of its secretory nature. The pendent male flowers of most species of *Phyllanthus* are furthermore hardly capable of holding any sizeable quantity of nectar.

Evidently Michaelis, in drawing up his "staminodial" theory of the disk, has leaned too strongly on evidence from the Crotonoideae. Baillon's ex-

plicit statement (1858: 127) that there are never any staminodes in the female flower of the Phyllanthoideae appears to be essentially correct (excepting *Phyllanthus acidus*). If Michaelis's observations of the Crotonoideae are correct, then it would appear that the disk in that subfamily is by and large not homologous with that in the Phyllanthoideae. Further research must be done in the Crotonoideae to reconcile the conflicting accounts of Michaelis and Baillon.

If the possibility of staminodial origin of the disk in *Phyllanthus* is rejected, the "emergence" theory remains to be examined. It is quite possible, as Baillon and Eichler suggested, that the disk is purely an expansion of the torus, as it appears to be in such families as the Cruciferae. However, the striking topographical arrangement of the disk-segments suggests another possibility. In the genera of Phyllantheae in which a corolla is developed (e.g., *Andrachne, Astrocasia*) the disk-segments are opposite the petals, not alternate as they would be if they represented the outer staminal whorl. In *Phyllanthus*, where the corolla is absent, the disk-segments (if free) occupy the same relative position as the missing petals (i.e., alternate with the calyx-lobes). This suggests that the disk may belong to the corolline whorl. In *Andrachne* and some of the primitive species of *Phyllanthus* (e.g., *P. polygonoides*) the disk-segments are more or less bifid (cf. Michaelis, pl. 1, fig. 1). Their appearance and antepetalous position suggests that the disk-segments in these plants may be "ligular" appendages of the petals corresponding to the "Nebenkrone" of the Caryophyllaceae. The production of glandular appendages by the floral leaves can hardly be considered remarkable in a family such as the Euphorbiaceae, where glandular structures are commonly associated with the basal portions of foliage leaves and bracts. Nor can the usual lack of vascular supply to the disk be considered surprising when it is recalled that the suppressed petals have left no rudimentary vascular traces either. However, at present it is really not possible to decide whether the disk-segments should be considered toral expansions or corollar appendages; the simple structure of the disk does not offer any clues definite enough to choose between the two alternatives.

Androecium.

According to Michaelis (1924: 121) the primitive androecium in the Euphorbiaceae is one of many stamens in several whorls; he found no evidence of phylogenetic increase in stamen number except in a few anomalous cases such as *Ricinus*. In *Phyllanthus* reduction from a polymerous androecium to one with few stamens may be traced in at least two phylogenetic lines, one of which is in the West Indies. *Phyllanthus discolor* (sect. *Williamia*) has ten to fifteen stamens with the filaments connate and the anthers spirally disposed or in three whorls; this is the highest stamen number found in any New World species. *Phyllanthus microdictyus*, the other species of sect. *Williamia*, has six to ten stamens in two or three whorls (the filaments being connate in all these related species). In sects. *Williamiandra* and *Orbicularia*, which are clearly derived from sect.

Williamia, the stamen number is mostly six, but in *P. phlebocarpus* of the latter section it is reduced to three. There can be little doubt that these species are related and that there has been a progressive reduction in stamen number during the evolution of the group. However, sect. *Williamia*, because of its phyllanthoid branching and areolate pollen grains, cannot be one of the most primitive groups in the genus. Furthermore, in sect. *Elutanthos*, which appears to be the progenitor of *Williamia*, the stamens are never more than three; and this small number also characterizes the vegetatively primitive species of sect. *Paraphyllanthus*.

Section *Polyandroglochidion* of New Caledonia, with up to fourteen stamens, is the only other group with over ten. In this group the pollen grains are colporate and the stamens free, but vegetatively the representatives have the specialized phyllanthoid branching. On the basis of the existing species of *Phyllanthus*, therefore, it would appear necessary to postulate an increase in stamen number from the three to five of primitive sections like *Paraphyllanthus* and *Menarda* to the ten or more of *Williamia* and *Polyandroglochidion*. That this is not impossible is apparent from the fact an undoubted increase in carpel number has occurred in a few cases. However, another and perhaps more likely possibility is that the various groups of *Phyllanthus* are descended from an ancestor — now extinct — which had a polymerous androecium combined with unspecialized branching. Evolution of the living representatives of *Phyllanthus* from such an ancestor would render unnecessary any hypothesis of increase in stamen number.

In the vast majority of the species of *Phyllanthus* the stamen number is six or less. Androecia of two, three, or four stamens have doubtless evolved by reduction from hexamerous and pentamerous ones such as those of sects. *Chorizandra* and *Anisonema*, respectively. More or less concomitant with reduction in stamen number are the two tendencies toward: (1) coalescence of stamens, at first by the filaments and then by the anthers; and (2) displacement of the line of anther dehiscence from vertical to horizontal.

Among the West Indian species, the introduced *P. tenellus* has the least-modified androecium, of five free stamens. In sect. *Cicca* there are four free stamens, and in sect. *Loxopodium* three. In the rest of the sections (except in relatives or descendants of sect. *Williamia*) there are either two or three stamens which are usually connate. In the most highly evolved androecia the anthers are oriented so that the line of dehiscence is horizontal and in sect. *Epistylium* they are deflexed so as to appear upside down.

Mueller depended heavily on these differences in stamen number and direction of anther-slits in distinguishing sections of the genus. Bentham (1878) rightly criticised this as leading to an unnatural classification; but Mueller was not unaware of the artificiality of the dehiscence character. The use of anther characters appears to have been largely a matter of expediency on the part of Mueller. Unfortunately for those who have subsequently had occasion to consider the subgeneric classification of

Phyllanthus, this character has proved to be a poor choice not only because of the violence it does to relationships but also because of its ambiguousness. Baillon (1858: 112) had already observed: "Je ne connais pas chez les Euphorbiacées, quoi qu'en disent quelques descriptions, d'examples positifs de dehiscence transversale." As Baillon realized, the anthers in *Phyllanthus*, as in other Euphorbiaceae, nearly always open longitudinally with respect to their own axes; most "transversely dehiscent" anthers merely have been bent onto the horizontal plane without the line of dehiscence changing relatively to the long axis of the anther. Nevertheless, there is in some species at least a partial displacement of the dehiscence-plane; the slits of the anther sacs, instead of being perfectly parallel, come together on the abaxial face and are confluent in a single arc. This type of dehiscence may be truly "oblique" but in practice the distinction is excessively subtle. The reader of the descriptions in this work may assume that the anthers open by slits that are longitudinal or nearly so, and that the stated direction of dehiscence will apply in relation to the long axis of the flower rather than to the anther itself.

The final product of the trend towards reduction and coalescence of the stamens has been reached in those species of *Phyllanthus* in which the stamens with horizontally dehiscing anthers are completely fused, so that the androecium presents the appearance of a single stamen with a peltate anther that dehisces all the way around the circumference. This remarkable compound structure, or *synandrium*, characterizes all the species of the West Indian sect. *Cyclanthera* and occurs also in the Cuban *P. dimorphus* and in two species of Madagascar (Leandri, 1938). Personal examination of the Madagascarian *P. ivohibeus* has shown that this species, like *P. dimorphus*, belongs to sect. *Phyllanthus*. Possibly these two species are related so that the synandrium evolved only once within sect. *Phyllanthus*. But in any event the synandrium must have developed independently in the very different sect. *Cyclanthera*. Since many species of *Phyllanthus* have an androecium of three stamens with the anthers sessile atop a column, the independent origin of the synandrium can actually be accounted for rather easily on mechanical grounds; all that is required is fusion of the connectives and coalescence of the anther-slits.

The study of the androecium for taxonomic purposes, i.e., with the intention of finding "key" characters, is attended with the difficulty that the filaments are very late in developing. The conspicuous staminal column of the mature male flower may be scarcely evident in the bud, and stamens which actually are connate by the filaments may be interpreted mistakenly as free. This rapid expansion during anthesis also characterizes the styles of many species and should be kept in mind by anyone who is drawing up or attempting to use a description.

Anatomically the stamens of *Phyllanthus* offer little of interest, at least in the forms which have been investigated. Each stamen is supplied with a single trace of slender tracheids which in the connective may bifurcate or end entire. The traces of the individual stamens remain separate in the staminal column. The anthers, unlike those of many other Euphorbi-

aceae, have no special vesture or glandular development. The connective undergoes a number of modifications, being enlarged and emarginate between the anthers in some South American species and apiculate in several Old World species; but in our West Indian representatives it is unspecialized.

Pollen grains.

One of the most striking discoveries made during the study of the West Indian species of *Phyllanthus* was the extraordinary diversity of pollen morphology within the genus. Erdtman (1952) reported for the first time the characteristic pollen grain of subg. *Xylophylla*; but by a curious circumstance, all of the four species he reported on happened to have areolate grains, and he apparently was unaware of the great intrageneric variability. During the present study the pollen of about one-third of the species in the genus has been examined, including many Old World species and at least one species from all except one or two sections. Although a number of phylogenetically critical species have so far not been investigated (due to lack of material), the general lines of pollen morphology within *Phyllanthus* are now apparent.

Erdtman's general discussion of pollen morphology and his special treatment of the Euphorbiaceae have provided much assistance and stimulation during examination of the pollen of *Phyllanthus*. However, his very complex terminology appears not only unwieldy but also needlessly complicated as far as the needs of systematists, rather than palynologists, are concerned. Much of the terminology in the following discussion has consequently been adopted from that proposed by Faegri and Iversen (1950).

The small size of the microspores of *Phyllanthus* is doubtless partly responsible for their being so poorly known. They average around 20μ in diameter, and grains over 30μ broad are rare. Observation under an oil immersion lens is usually necessary to determine the ornamentation pattern of the exine. The use of pollen characters is therefore not practicable for routine determinations; but it is an invaluable aid in assigning species to their place within the genus.

The commonest and probably the basic type of pollen grain in the Phyllanthoideae and some of the tribes of Crotonoideae much resembles those in such families as the Flacourtiaceae, Sapindaceae, and Celastraceae. It is subglobose or broadly ellipsoidal and thin-walled, with a reticulate exine. In most cases the reticulum is sharply defined and raised, so that the ornamentation of the exine falls into the "OL" pattern of Erdtman (1952: 22), i.e., the spaces between the walls (muri) of the reticulum are dark at the outermost focus and bright at the inner focus. In the grains of many species of *Phyllanthus* the reticulum is so fine that it can scarcely be resolved even under oil immersion. The exine is provided with three longitudinal furrows (colpi) which usually have median round or elliptic germ-pores (ora). Both Erdtman and Faegri and Iversen have applied the term "tricolporate" to grains of this type.

Tricolporate pollen grains are characteristic of the presumably primitive petaliferous genera of Phyllantheae such as *Andrachne* and *Savia*, and of the apetalous genera more closely related to *Phyllanthus* such as *Securinega* and *Flueggea*. In *Phyllanthus* such grains occur in a number of groups, including sects. *Paraphyllanthus* and *Phyllanthus* (PLATE-FIG. 35). In several species, including those of sects. *Loxopodium*, *Urinaria*, and part of sect. *Phyllanthus*, the microspore is very similar except that there are four colpi instead of three. *Phyllanthus niruri* (PLATE-FIG. 34) has unusually large prolate grains which (like some other species of sect. *Phyllanthus*) have a "heterobrochate" exine, the reticulum being much coarser midway between the colpi than along their margins. In most species, however, there is no such striking difference in the fineness of different parts of the reticulum.

The majority of the species native to the West Indies have a type of pollen grain very different from that just discussed. It was illustrated by Erdtman (1952: fig. 97a) and described by him as "synrugoidorate," i.e., "provided with rugoid streaks surrounding angular (usually 5-angular) areoles." In the present work these grains will be referred to as "areolate" (PLATE-FIGS. 41 & 42). All such grains are spherical and quite similar in ornamentation, differing mainly in size and in the number of areoles. At each corner of the areole, where three furrows come together, is a circular germ-pore. There is a distinct and continuous exinous ridge which bounds the perimeter of the areole and at the same time defines the edge of the furrow; it is formed by the amalgamation of the minute club-shaped sculptural elements of the exine ("pila" of Erdtman, "clavae" of Faegri and Iversen). Within the areole, the clavae form a reticulum which is very much like that of ordinary colporate grains.

Areolate pollen grains of the kind just described are known only from New World species of *Phyllanthus*. However, areolate grains that superficially are very similar occur in the Old World species of sect. *Macraea;* Erdtman, in fact, noted no essential difference between the grain of the West Indian *P. mimosoides* and the Hawaiian *P. sandwicensis* [= *P. distichus*]. But close examination shows that in the latter the ora are located midway between the angles of the areoles and thus in the middle of one furrow rather than at the intersection of three of them (PLATE-FIG. 43). A similar kind of pollen grain occurs in the Indo-Chinese species *P. ruber*, whose affinities are rather doubtful. From various lines of evidence it is clear that the Old World species with areolate grains are not closely related to the New World species; apparently the areolate ornamentation has evolved quite independently in the two groups.

A third kind of areolate microspore occurs in the West Indian sect. *Cyclanthera*. It resembles the other two except for the fact that the reticulum within the areole is reduced to a single brochus.. The areole therefore appears to have a median pore (or plug, depending on the plane of focus) and may be referred to as "foveolate" (PLATE-FIG. 40). It is evident from various considerations that sect. *Cyclanthera* is derived from

sect. *Callitrichoides*, and that its foveolate grain must be derived from the grain of the latter, which has ribbon-shaped areoles that give the exine a striate appearance (PLATE-FIG. 39). It is at present impossible to be sure if the "banded" grain of sect. *Callitrichoides* is derived from the areolate grain of other West Indian species. It might have evolved independently; but the relationships of sects. *Cyclanthera* and *Callitrichoides* are too obscure to decide the matter.

There are a number of other kinds of pollen in *Phyllanthus* which fall into neither the areolate nor the ordinary colporate type. In sect. *Nothoclema,* for instance, the colpi are greatly shortened to dumbbell-shaped furrows with a germ-pore at each end, and the exine is markedly echinulose ("pilate" in Erdtman's terminology) (PLATE-FIG. 36). The spherical grain of the introduced *P. pulcher* (sect. *Eriococcus*) has no evident furrows, or areoles, and the reticulum is broken only by equidistantly placed pores (PLATE-FIG. 44).

The diversity of pollen types in *Phyllanthus* is thus so great that it becomes difficult to interpret the possible evolutionary relationships between the different kinds. Erdtman has designated as "breynioid" the pollen occurring in the "subtribes" Glochidiinae, Phyllanthinae, and Sauropodinae. As found in *Breynia* the pollen grain is more or less oblate with several (7 to 10) furrows, each having two ora, and a prominent reticulum set off from the furrow by a definite border. Well-marked breynioid grains have been observed in *Phyllanthus* only in the South American species of sect. *Microglochidion* (PLATE-FIG. 38). However, there is no sharp dividing line between breynioid and ordinary tricolporate grains; in *Glochidion*, for instance, the few species investigated have four-colporate grains which hardly differ from those of many species of *Phyllanthus*.

Erdtman (op. cit. 174) has attempted to relate the breynioid grains of *Breynia* and *Sauropus* to the 4-colporate grains of *Glochidion* on the one hand and to the "synrugoidorate" grains of *Phyllanthus* on the other. This idea has been confirmed, in a general way, in the present study. In sect. *Anisonema* (e.g., *P. reticulatus*) and several Old World groups, the microspore has three colpi which are conspicuously margined and confluent at the poles. If the number of colpi should be increased to five or six and their intersection at the poles be precluded by spatial conditions, the colpi might terminate instead at the margins of the two polar areoles thus formed. The result might be a pollen grain with relatively few large areoles, such as that of *P. subcarnosus* (PLATE-FIG. 41). Further specialization might lead on the one hand, by multiplication of the number of areoles, to the "poly-areolate" grains of many West Indian species, and on the other hand, by suppression of the furrows, to the porate grains of sect. *Eriococcus*. The areolate grain is thus nothing more than a breynioid grain with lateral connections at the ends of the furrows.

Erdtman's suggestions as to the morphological relationships of the pollen grains within the Phyllanthinae thus appear to be sound; but his speculations as to the origin of the "crotonoid" grain are less fortunate. He suggests that the polygonal pattern underlying the "crotonoid" ornamentation

of the grains of *Suregada zanzibarensis* indicates derivation from phyllanthoid pollen. According to this view, the grain of *Suregada* represents a transitional stage between that of *Phyllanthus* and that of *Croton* or *Jatropha*. It is very hazardous, however, to attempt to relate the microspores of genera as far removed as *Phyllanthus* and *Croton;* there is scarcely the slightest possibility that the latter genus is descended from the Phyllanthinae. It appears far more likely that crotonoid pollen grains have been derived from tricolporate types within the Crotonoideae. It is plain from the results of the present study that since very different pollen types may exist within closely related groups, comparisons between widely separated genera in a family such as the Euphorbiaceae are very liable to be unsafe.

Gynoecium.

The majority of the species of *Phyllanthus* have the typical euphorbiaceous gynoecium of three united carpels, and in common with all the Phyllanthoideae have a pair of collateral ovules in each locule of the ovary. In a few species, none of them native to the New World, the number of carpels is higher. The commonly cultivated *P. acidus* has a variable carpel number, fruits with three and with four locules being almost equally common. In sect. *Anisonema* the number fluctuates from three to ten, and Mueller (1866: 344) reported up to twelve locules in *P. reticulatus* (PLATE-FIG. 47). Otherwise, gynoecia with more than three carpels have been reported only in *P. ruber* (sect. *Nymphanthus*) and *P. buxifolius* (sect. *Scepasma*). It seems significant that the greatest variability in carpel number is concentrated in the single section *Anisonema*. Since the flowers in this section are otherwise basically pentamerous, it appears that in sect. *Anisonema* and groups derived from it evolution has proceeded from a five-carpellate gynoecium by reduction to three, and by multiplication to several carpels. Michaelis (1924: 120) recognized that the gynoecium has undergone both multiplication (e.g., *Hura*) and reduction (e.g., *Antidesma*) in sporophyll number, whereas he found no evidence of multiplication of sporophylls in the androecium.

During the preparation of the present study, a number of difficulties in the terminology of the gynoecium have been encountered; these are mostly due to the conflicting definitions in the literature. Hanf (1934) has proposed a new classification of terms which contains some drastic changes of concept; his system has been explained in translation by Just (1939). According to Hanf's view, each carpel of the angiospermous flower is terminated by a *stylodium*; the term "style" is restricted to apply to the elongated portion of a "coenocarpous" ovary (i.e., one with united carpels). The application of this concept gives the corollary that a single flower can have no more than one style; and in such families as the Ranunculaceae and Caryophyllaceae styles are considered to be absent, flowers of these groups having stylodia only.

Hanf's study of stylar morphology has the great merit of clarifying the relationships between various stylar apparatuses that have become ob-

scured through careless use of terms. However, his definitions are directly contradictory to those current in most systematic works. It seems worth while, therefore, to examine the propriety of adopting such a radically different terminology.

The word "stylodium" was apparently coined by Grisebach in his textbook "Grundriss der sytematischen Botanik" (1854). His discussion (in translation) is as follows:

> "The boundary between style and stigma is actually established morphologically by the stylar canal, but the designation style and style-arm (rami styli) is applied in systematics to all cylindrical carpel apices, and the [term] stigma is restricted to the glandular part of them. It is therefore appropriate to distinguish the style-like stigmas as stylodes (stylodium) from the true stigmas which are physiologically characterized by their reaction to the pollen grains. According to this definition, for example, the monocarpic pistil of the grasses has one style, two stylodia, and [two] stigmas."

Grisebach (op. cit.) described the gynoecium of *Euphorbia* as having "stylo tripartito, stylodiis bifidis." In his description of *Cicca antillana* (1857) he still used the term stylodium, but by 1859, in the "Flora of the British West Indian Islands," he had abandoned it. Since the term has not been recently used in systematic literature, the force of custom and usage would appear to weigh against its adoption unless there should be compelling reasons for doing so.

It must be admitted that the word "style" has not always been used with precision. Gray ("Structural Botany," 1879) defined it as the "usually attenuated portion of a pistil or carpel between the ovary and stigma." In the sense of Gray, therefore, the word is a topographical designation and does not imply specific morphological value. The definition given by Fernald (1950): "the usually attenuated portion of the pistil connecting the stigma and ovary" breaks down when applied to a gynoecium with united carpels but free styles.

Baillon (1858) held a similar concept during his studies on the Euphorbiaceae, for he described the stigma-bearing structures in terms of the style and its branches. Mueller Argoviensis, in his work for the "Prodromus," at first (1863) described the style of the Euphorbiaceae as " . . . varius, saepius brevius et in tot ramos divisus quot loculi ovarii." But in his generic description of *Phyllanthus* in the finished monograph (1866) he stated: " . . . styli loculis ovariorum isomeri." Mueller thus came to regard the style as the prolongation of the individual carpel rather than of the entire pistil, as he had at first. Pax and Hoffmann (1931) followed the same concept in describing the styles of the Euphorbiaceae as "frei oder verwachsen, wenn frei, dann meist 2-, seltener vielspaltig."

It appears that at least in the Euphorbiaceae the usage of Mueller is perfectly clear and accurate. The style may be defined as the attenuate portion of the carpel (not the pistil) between the ovary and stigma. When the styles are united, as they often are in the Euphorbiaceae, the compound structure may be termed the *stylar column*. The result of this

definition is that the stylar column, not the style, of *Phyllanthus* is the morphological equivalent of the style of the Labiatae. Any possible confusion may be obviated, however, by qualifying the latter organ as the "compound style."

The styles of *Phyllanthus* exhibit a remarkable latitude of variation in form, but they may be classified roughly into two types which become distinct at an early stage of development in the bud. In all species investigated the carpel at first is cupuliform with a horseshoe-shaped margin. In one case the adaxial portion of the rim early takes on the form of a "Y" and the carpel apex (i.e., the style) grows out more or less bifid. In the other case the rim retains its original shape longer, and the style is either entire or dilated into an adaxially channelled crenulate or lacerate expansion, the stigma. Since the stigma is not always well-defined, particularly in styles of the first type where the stigmatic surface is discontinuous, the *style-branch* is often the most convenient term.

The great variations in the mature stylar apparatus in different species are the result of the interactions of three growth processes: (1) the differentiation of the embryonic carpel apex into "bifid" or "entire" styles; (2) the relative amount of longitudinal vs. transverse growth; and (3) the degree of union between the styles. Many different recombinations of these three processes occur. The styles may be completely united into a column as in *P. ovatus* (sect. *Hemiphyllanthus*) or almost completely free as in sect. *Paraphyllanthus;* the stigmas may be scarcely defined in many species with slender bifid styles, or greatly dilated to form a calyptra as in *P. mirificus*. In species with dilated style-tips, the original adaxial margins of the hippocrepiform embryonic carpel are represented by a pair of adaxial auricles. Usually these are small and sometimes even obsolete, but in some species (e.g., *P. excisus*) they may be quite prominent. In a general way the auricles mark the point at which the stylar column ends (when the styles are connate) and the stigmatic surface begins. Below the auricles the stigmatic tissue is usually embedded in the center of the style or stylar column and is represented externally only by a slender adaxial suture. Internally, the loose conducting tissue of each style becomes confluent at the point where the tops of the ovarian parts of the three carpels are fused. In most species of *Phyllanthus* a prolongation of this tissue runs into the top of each locule and forms a cap-like structure, the *obturator,* which is closely appressed to the micropylar ends of the ovules (PLATE-FIGS. 48 & 49). Baillon (1858), who first applied the name obturator to this prolongation of the stylar tissue, recognized within the present limits of *Phyllanthus* two types of obturators: a single one over both ovules of a locule in *P. salviaefolius* (sect. *Oxalistylis*) and an obturator for each ovule in "P. grandiflorus" (identity uncertain). Examination of material in the present study has disclosed in every case a common obturator for both ovules, but its relative development and orientation appear to vary a good deal from species to species. It conspicuously overtops the ovules in *P. subcarnosus* but is nearly vertical in *P. polygonoides* (PLATE-FIG. 49). Unlike *Ricinus*, in which Baillon

reported traces of the obturator in the mature seed, the organ is transient in *Phyllanthus* and atrophies during maturation of the fruit.

The vascular supply of the carpel is quite similar in most of the species of sect. *Phyllanthus* investigated, but needs to be studied in other groups. At the base of the ovary the carpellar bundle divides into one dorsal and two ventral traces. The dorsal trace ramifies into a reticulum on the dorsal surface of the carpel, while the two ventral traces run vertically. The latter first give off the ovular traces and then abruptly bend abaxially and run obliquely across the lateral face of the carpel to join the dorsal reticulum near the base of the stylar column. The resulting compound bundle then enters the stylar column and bifurcates, each branch forking or remaining unbranched, depending on the character of the style-tips. The point at which the ventral traces leave the axis of the ovary and bend outwards is well-marked by a sharp discontinuity in the tissue, and the upper third of the axis is without vascular supply. The courses taken by the vascular bundles determine to a great extent the configurations of the carpels in the dehisced fruit. The portion of the axis beneath the "bending-point" of the ventral traces becomes the *columella,* which remains after dehiscence of the fruit as a column projecting from the center of the calyx. The obliquely ascending ventral traces on the lateral faces of the carpels determine the upper line of dehiscence of the cocci, which split on the lateral faces along lines curving away from the ventral traces.

Baillon (1858: 139–140), partly on the basis of his ontogenetic studies, considered the ovules of the Euphorbiaceae to be borne by the axis. From a merely topographic point of view it is correct to say the ovules are "axile," but this need not imply that they are inserted on a structure of "stem" or "branch" nature. The columella, which looks so much like a prolongation of the torus, has no vascular supply independent of the ventral traces, and its extent is exactly determined by the distance these travel vertically before turning outward. The columella is therefore a compound structure derived from the basal parts of the fused ventral margins of the carpels, and is morphologically equivalent to the central placental column of the Caryophyllaceae of the "free-central" placenta of the Primulaceae. There is no evidence to support the assertion of Lam (1948) that the Euphorbiaceae are a "stachyosporous" family (i.e., with sporangia borne on modified branches); the gynoecium of *Phyllanthus* is not fundamentally different from that of families admitted by Lam to be "phyllosporous."

In *Phyllanthus* each locule of the ovary contains a pair of usually collateral anatropous pendent ovules. The funicle of the ovule is sharply deflected downward from the top of the columellar part of the axis (i.e., about one-third of the way down from the top of the locule), and the hilum is on the side of the ovule toward the center of the ovary. The ovule is more or less barrel-shaped with two integuments, the outer of two cell-layers, the inner of three. The nucellus in all species examined is at least slightly prolonged beyond the exostome of the micropyle as a more or less clavate beak which fills up the space between the micropyle and

the obturator (PLATE-FIG. 49). In species with a relatively massive obturator such as *P. subcarnosus* the nucellar beak, though well-developed, does not project very far beyond the micropyle, but where the obturator is short the tip of the nucellus may be strikingly elongated. In all observed cases there is an intimate contact between obturator and nucellus. The embryo sac, according to Maheshwari and Chowdry (1937), is the normal eight-nucleate type.

Baillon (1858: 613) pointed out that in sect. *Anisonema* the ovules, thought at first collateral, later become obliquely superposed as in *Glochidion*. This change of ovular position is probably due to spatial conditions, since the large number of locules results in a diminished average volume of each one (PLATE-FIG. 47). In all of the three-carpellate gynoecia examined, the ovules are collateral without exception.

Fruit.

In the great majority of the species of *Phyllanthus* the fruit is a dry thin-walled capsule which often dehisces explosively at maturity. The wall of the fruit is ordinarily composed of two distinct layers which are distinguishable from a rather early stage of the ovary (PLATE-FIGS. 48 & 49). The exocarp, which contains all the vascular supply, is usually thin, scarious, and greenish or reddish at maturity of the fruit; it covers only the outer tangential (abaxial) wall of each coccus. The yellowish endocarp, which lacks vascularization, has a heavily sclerified thick dorsal (tangential) wall and much thinner lateral (radial) walls (PLATE-FIG. 50). When the capsule dehisces, the carpels (now cocci) first separate from one another and from the columella; then the lateral walls split open along an arc as described previously. Often the endocarp also splits vertically along the middle of the dorsal valve, so that the coccus has the form of an irregularly four-valved box loosely enclosing the pair of seeds.

There are a number of species, however, in which the exocarp of the fruit remains fleshy until rather late in ontogeny (e.g., *P. juglandifolius*). In others the exocarp never dries up, and the fruit is either baccate or drupaceous, depending on the degree of sclerification of the endocarp. In *P. reticulatus* (sect. *Anisonema*), which has a baccate fruit, the endocarp is not only tenuous but is not clearly differentiated from the exocarp (PLATE-FIG. 47). In *P. emblica* the ripe fruit is drupe-like with a fleshy exocarp and bony endocarp, but when the fruit eventually dries up the endocarp separates into three massive cocci. The fruit of *P. elsiae* is at first fleshy but on drying the exocarp becomes pithy, while the endocarp is sclerified but thin. In the related *P. acidus* the massive endocarp is bony and indehiscent while the exocarp remains fleshy, so that in this species the fruit is a true drupe with a three- or four-celled putamen. Mueller's description (1886: 413) of the fruit of sect. *Cicca* as capsule-like with two-valved cocci was due to his mistaken inclusion of the very different genus *Margaritaria* in the same section with *Cicca*.

In a general way the type of fruit (i.e., whether dry, baccate, or drupaceous) is definitely related to the habit of particular species. The her-

baceous annual species all have an explosively dehiscent capsule which falls away from a persistent calyx. The shrubby species tend to have a more tardily dehiscent capsule which may fall with the pedicel and columella still attached, and in *P. reticulatus* and *P. subcarnosus* the fruit is fleshy. Finally, in *P. acidus*, *P. elsiae*, and *P. emblica*, all of which are trees, the fruit is drupaceous or "woody." This unmistakable correlation between relative explosiveness of fruit and life-span of plant nicely illustrates adaptation in dispersal capacity which must have a basis in natural selection. It also indicates that fleshiness of fruit *per se* may not always be a reliable mark of affinity, and is consequently of little value as a generic character.

Seed.

Usually there is a pair of seeds in each cell of the fruit of *Phyllanthus*, each of which has a trigonous outline due to compression against one another and the locule walls. Sometimes, however, only one of the seeds will attain full size, and the other will be under-developed. In sect. *Cicca* the relative development of the pair of seeds is most variable, for there may be either two equal seeds, one large and one small, or one large one only; and locules in which these three types occur may be found in a single fruit. In *P. emblica* the seeds of a pair are unequal, but both appear viable. Swartz (1800) characterized the seeds in the fruits of the West Indian sect. *Epistylium* as "subsolitaria"; this may be correct, but in the other native West Indian species there are nearly always two equal seeds in each locule. The tendency towards abortion of one of the ovules, which is also noticeable in the genus *Savia*, indicates the existence of a reduction trend toward the uniovulate condition of the Crotonoideae. However, in all of the Phyllantheae so far investigated the suppression of the second ovule takes place late in ontogeny, probably after anthesis; even though a locule of the mature fruit may have only one seed, examination of the ovary at an early stage has always shown two ovules in each cell.

The development of the seed-coat from the integuments appears to be somewhat variable and requires further investigation. The epidermal layer of the outer integument usually becomes variously modified during maturation of the seed; the resulting diversity in ornamentation of the testa provides convenient taxonomic characters for recognizing or distinguishing many species. Only rarely is the seed-coat quite smooth and uniformly colored as it is in *P. hyssopifolius* (PLATE-FIG. 57). In *P. juglandifolius* the seed-coat, although smooth, has a mottled appearance somewhat like that of *Ricinus* (PLATE-FIG. 64). Many different species have the seed-coat covered with raised dots, or points, which may be regularly or irregularly arranged; seeds of this type may be termed verruculose (PLATE-FIGS. 51, 52, 59). A great number of other species have seeds which though nearly smooth are seen under a lens to be covered with fine lines or ridges, on close inspection. Often the epidermal cells, which usually have their long axes transverse to the long axis of the seed, are so translucent that the cells of the subepidermal layer (which run

parallel to the long axis) show through. This gives the effect of logitudinal striae crossed by very fine striolae (PLATE-FIG. 55). In some of the herbaceous species of sect. *Phyllanthus* the seed-coat is very highly specialized. When the seeds of *P. junceus*, *P. echinospermus*, or related species, are placed in water they change from finely ridged or striate to "hispid" in appearance. Microscopic examination shows that this reaction is due to peculiar hygroscopic epidermal cells which are heteropolar: one end has conspicuously uneven wall-thickenings which give the lumen a scalloped outline, while the other is smoothly and less massively thickened. Slightly excentric toward the "smooth" end is a median peg of cellulose which runs through the lumen between the tangential walls. When the seed is wetted the longer unevenly thickened cell-ends swell out on the adaxial side and assume the form of concave arcs, while the shorter ends remain appressed to the surface of the seed; the projecting ends thus give the appearance of trichomes projecting from the seed-coat. This behavior presumably allows greater penetration of water into the seed-coat and consequently earlier germination of the seed. Such an adaptation, combined with the explosively dehiscent capsule, affords these herbaceous species a highly efficient mechanism for rapid dispersal and ecesis.

The seed of *P. urinaria* has a curious and unique kind of seed ornamentation (PLATE-FIGS. 53 and 54). The seed-coat is not only provided with sharp transverse ridges, but it has in addition deep pits on the sides; this combination of characters makes the seeds of *P. urinaria* unmistakable among those of the West Indian species. The deep pits on the radial walls perhaps represent a different sort of adaptation for permitting rapid penetration of water and faster germination.

In *P. orbicularis* developmental study has clearly shown that the heavily sclerified "palisade" layer of the seed-coat is developed from the outer layer of the inner integument (PLATE-FIG. 50); it is this layer which imparts to the seed most of its mechanical strength. In *P. orbicularis*, the middle layer of the inner integument is very inconspicuous in the seed, but the inner layer, though not enlarged, stands out because the cells are all filled with tannin. It will be noted that in this species, the two layers of the outer integument are relatively unimportant and not noticeably specialized. Too few species have been studied to know if the ontogeny of the seed is similar in every species; it is possible that in some species the sclerified layer is derived from the inner layer of the outer integument, but this remains to be demonstrated.

The mature embryo, which is embedded in rather copious whitish cartilaginous endosperm, ordinarily has a slender terete radicle and broad foliaceous cotyledons (e.g., in *P. juglandifolius*). In some of the herbaceous species (e.g., *P. amarus*), however, the cotyledons are narrowly oblong and only slightly broader than the radicle. Sometimes the embryo is slightly curved; Gaertner (1791: 125, pl. 108) described and illustrated the seed of *P. maderaspatensis* as having a "subspiral" embryo. Gaertner (op. cit. 127, pl. 109) clearly distinguished *Glochidion* on the basis of its very distinctive seeds, in which the seed-coat is fleshy and the hilar cavity

so enormously enlarged that the embryo is deformed; unfortunately, he chose to describe the genus under Banks' manuscript name *Bradleja*. This seed character, so clearly pointed out by Gaertner, is one of the best features for distinguishing *Glochidion*. Unfortunately, it has been passed over in recent years, with the result that the boundary between *Glochidion* and *Phyllanthus* has appeared weaker than it actually is.

CYTOLOGY

The cytology of *Phyllanthus* remains one of the poorest known areas of the morphology of the genus. Perry (1943), in the only previous specific contribution to the cytology of the Phyllantheae, found a diploid number of 28 in *P. caroliniensis* and *P. emblica;* he suggested that the basic number is 7 and that these species are therefore tetraploids. On the basis of his finding a diploid number of 56 in *Breynia*, he concluded that the latter is closer to *Phyllanthus* than one would judge from the treatment of Pax and Hoffmann (1931); evidence from other fields tends to support his statement. On the other hand Perry observed a diploid number of 16 in *Securinega obovata* [= *Flueggea virosa*]. This apparent difference in base-number indicates that further investigations in the Phyllantheae should produce interesting data for purposes of determining evolutionary relationships.

The only additional species whose chromosome number has been investigated is *P. juglandifolius* (sect. *Asterandra*), root-tip preparations of which were made by Dr. E. G. Voss from material in the University of Michigan Botanical Gardens. The diploid number as seen in root-tip smears of this species is approximately 160; the number is so large that both of us could agree only that it lies between 20n and 24n (assuming 7 as the basic number), and is probably closer to 168 than to 140. Although one can scarcely draw any far-reaching conclusions on the basis of the chromosome complement in only three species out of 650, the very high chromosome number in *P. juglandifolius* is quite suggestive. It indicates that amphidiploidy might have occurred repeatedly during the evolution of the West Indian species related to sect. *Asterandra*, and raises the possibility that the difficulty in determining relationships within the genus may be due to ancient hybridizations between rather widely separated species. Cytological examination of additional species from tropical America can hardly fail to throw considerable light on the difficult problem of intrageneric relationships. Unfortunately all efforts to germinate seeds of the shrubby species of sects. *Elutanthos*, *Williamia*, *Orbicularia*, and *Thamnocharis* have been unsuccessful. Collection of cytological specimens in the field may be the only means of successfully attacking the problem.

Perry has concluded from his data that "it appears that the direction of evolution in this family has been from the annual to the perennial condition, as was found for the Crassulaceae, Leguminosae, Ranunculaceae." Apparently he was impressed by the fact that some of the herbaceous species have lower chromosome numbers than the woody ones. However,

on the basis of morphological evidence other than chromosomes there is no doubt that at least in *Phyllanthus* the annuals are definitely derived from shrubby or suffruticose ancestors; and this is surely true of the Euphorbiaceae as a whole. The higher chromosome number of woody species is itself not a reliable indicator of primitiveness; Stebbins (1950) and others have shown that the arboreous habit tends to favor polyploidy during the course of evolution.

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(*To be continued*)

EXPLANATION OF PLATES *

PLATE I. GROWTH FORM.

FIG. 1. *Phyllanthus platylepis* Small (grown from seed of *Webster 3651*, Levy Co., Fla.).

FIG. 2. *Phyllanthus pachystylus* Urb. (*Webster 3906*, Moa region, Cuba), 1/10 natural size.

FIG. 3. *Phyllanthus tenellus* Roxb. (cult. Univ. of Michigan Bot. Gardens), 1/4 natural size.

FIG. 4. *Phyllanthus juglandifolius* Willd. (cult. Univ. of Michigan Bot. Gardens).

PLATE II. BRANCHLET ANATOMY. (× 50)

FIG. 5. *Phyllanthus reticulatus* Poir. (*Webster 5237*, Jamaica); cross-section of branchlet slightly above the node. At the bottom of the picture is the petiole and the two stipules. FIG. 6. Section through nodal region, showing trilacunar node with lateral stipular traces.

FIG. 7. *Phyllanthus maleolens* Urb. & Ekm. (*Holdridge 1381*, Haiti [MICH]); cross-section of branchlet through nodal region, showing trilacunar node with large stipular traces.

* Voucher specimens are deposited at both the University of Michigan and Harvard University herbaria, except where another herbarium is specifically indicated.

FIG. 8. *Phyllanthus williamioides* Griseb. (*Webster 4014*, Cuba); cross-section of branchlet.

PLATE III. STEM ANATOMY. (× 50)

FIG. 9. *Phyllanthus botryanthus* Muell. Arg. (Harvard slide 2922, probably from *Curran & Haman 164*, Curaçao); cross-section of mature stem. FIG. 10. Tangential section.

FIG. 11. *Phyllanthus emblica* L. (Harvard slide 2120, Cuba); tangential section. FIG. 12. Radial section.

FIG. 13. *Phyllanthus pachystylus* Urb. (*Webster 3906*, Cuba); vessel elements.

PLATE IV. PHYLLOCLADES.

FIG. 14. *Phyllanthus* × *elongatus* (Jacq.) Steud. (*Webster s.n.*, cult. Harvard greenhouse); cross-section of penultimate axis, × 25. FIG. 15. Cross-section of ultimate axis, × 40. Both axes are still so young that the sclereids in the cortex are not yet hardened.

FIG. 16. *Phyllanthus epiphyllanthus* L. (*Jervis 1368*, Cuba); cross-section of phylloclade, taken from dried specimen, × 72. The dark brown masses represent the compacted remains of the tannin-filled cortical parenchyma cells. Note the concentric bundles.

FIG. 17. *Phyllanthus montanus* Sw. (*Webster 5637*, Jamaica); cross-section near tip of phylloclade, × 72. The structure on the right is a scale-leaf. Note that at this level palisade tissue is developed only on one side.

PLATE V. STOMATA (× 175)

FIG. 18. *Phyllanthus microdictyus* Urb. (*Webster 3809*, Cuba); in this, and the following figures, the upper epidermis is shown on the left-hand side of the figure and the lower epidermis on the right-hand side.

FIG. 19. *Phyllanthus heliotropus* Wright ex Griseb. (*Shafer 10708*, Cuba [US]).

FIG. 20. *Phyllanthus selbyi* Br. & Wils. (*Britton et al. 14157*, Isle of Pines).

FIG. 21. *Phyllanthus niruri* L. (*Britton et al. 6438*, Puerto Rico [NY]).

PLATE VI. LEAF ANATOMY.

FIG. 22. *Phyllanthus scopulorum* (Britton) Urb. (*Webster 3849*, Cuba); cross-section of nearly mature leaf, from specimen preserved in FAA, × 40.

FIG. 23. *Phyllanthus ekmanii* Webster (*Jervis 3650*, Cuba); cross-section of mature leaf, from dried specimen, × 35.

FIG. 24. *Phyllanthus microdictyus* Urb. (*Webster 3809*, Cuba); cleared leaf-blade, × 85.

FIG. 25. *Phyllanthus incrustatus* Urb. (*Shafer 4453*, Cuba [NY]); cleared leaf at focus just beneath upper epidermis, showing arrangement of sclereids. × 85.

FIG. 26. *Phyllanthus comosus* Urb. (*Webster 3883*, Cuba); marginal area of cleared leaf, × 85.

FIG. 27. *Phyllanthus formosus* Urb. (*Shafer 4102*, Cuba [NY]); marginal area of cleared leaf, × 85.

PLATE VII. Leaf venation. (× 50).

Fig. 28. *Phyllanthus emblica* L. (*Jack 4246*, Cuba).

Fig. 29. *Phyllanthus botryanthus* Muell. Arg. (*Triana 3664*, Colombia).

Fig. 30. *Phyllanthus reticulatus* Poir. (*Britton 4067*, Jamaica [NY]).

Fig. 31. *Phyllanthus chryseus* Howard (*Webster 3853*, Cuba).

Fig. 32. *Phyllanthus scopulorum* (Britton) Urb. (*Webster 3849*, Cuba).

Fig. 33. *Phyllanthus spathulifolius* Griseb. (*Webster 3896*, Cuba).

PLATE VIII. Pollen grains.*

Fig. 34. *Phyllanthus niruri* L. (*Ekman H16515*, Hispaniola [S]).

Fig. 35. *Phyllanthus trigonus* Urb. (*Ekman H2792*, Hispaniola [S]); polar view, outer focus.

Fig. 36. *Phyllanthus acuminatus* Vahl (*Wright 1938*, Cuba [S]); more or less equatorial view, outer focus.

Fig. 37. *Phyllanthus heliotropus* Wr. ex Griseb. (*Ekman 10735*, Cuba [S]).

Fig. 38. *Phyllanthus vaciniifolius* (Muell. Arg.) Muell. Arg. (*Sandwith 1315*, Br. Guiana [S]).

PLATE IX. Pollen grains.

Fig. 39. *Phyllanthus carnosulus* Muell. Arg. (*Wright "714"*, Cuba [GOET]).

Fig. 40. *Phyllanthus berteroanus* Muell. Arg. (*Leonard 8826*, Hispaniola [NY]); upper right-hand quadrant shows the appearance at outer focus.

Fig. 41. *Phyllanthus subcarnosus* Wr. ex Muell. Arg. (*Wright 1946*, Cuba [S]); insert shows the appearance of the grooves at outer focus (i.e., very narrow).

Fig. 42. *Phyllanthus maleolens* Urb. & Ekm. (*Ekman H6849*, Hispaniola [S]).

Fig. 43. *Phyllanthus distichus* Hook. & Arn. (*Degener 11645*, Hawaiian Islands).

Fig. 44. *Phyllanthus pulcher* Wall. ex Muell. Arg. (*Broadway 5459*, Trinidad [S]).

PLATE X. Floral anatomy.

Fig. 45. *Phyllanthus chryseus* Howard (*Webster 3853*, Cuba); longitudinal section of male flower bud, × 30.

Fig. 46. *Phyllanthus reticulatus* Poir. (*Webster 5237*, Jamaica); longitudinal section of male flower, showing stomatal pits in disk, × 30. Fig. 47. Cross-section of female flower, × 30.

Fig. 48. *Phyllanthus* × *elongatus* (Jacq.) Steud. (*Webster s.n.*, cult. Univ. of Michigan greenhouse); cross-section of ovary at the level of the obturators, × 45.

Fig. 49. *Phyllanthus polygonoides* Nutt. ex Spr. (*Webster & Wilbur 2965*, Texas); longitudinal section of ovary showing association of obturator and nucellar beak, × 100.

*The drawings in plates VIII and IX are semi-diagrammatic and (except for figs. 35, 36, and 40) indicate the appearance of the exine at roughly the level of the base of the individual sculptural elements (muri or pilae). All drawings are on the scale of 1 cm. = 5.9 μ.

FIG. 50. *Phyllanthus orbicularis HBK.* (*Webster 3867*, Cuba); longitudinal section of immature fruit, × 100. Above, ovary wall; in the center, two seeds showing the two cell-layers of the outer integument and the three of the inner.

PLATE XI. SEEDS.

FIG. 51. *Phyllanthus pudens* L. C. Wheeler (*Bush 906, Texas* [GH]); verruculose ornamentation, × 22.

FIG. 52. Ventral and radial view, × 7.

FIG. 53. *Phyllanthus urinaria* L. (*Cory 49975*, Texas [GH]); transversely barred ornamentation, × 45.

FIG. 54. Ventral and radial view, × 14.

FIG. 55. *Phyllanthus amarus* Schum. & Thon. (*Small & Small 6818*, Florida [GH]); finely (longitudinally) rbibed ornamentation, × 45.

FIG. 56. Ventral and radial view, × 14.

PLATE XII. SEEDS.

FIG. 57. *Phyllanthus hyssopifolius* HBK. (*Ekman H15612*, Hispaniola [S]), × 12.

FIG. 58. *Phyllanthus emblica* L. (*Jack 4246*, Cuba [NY]), × 6.

FIG. 59. *Phyllanthus niruri* L. (*Parks 14595*, Texas [GH]), × 12.

FIG. 60. *Phyllanthus williamioides* Griseb. (*Webster 4014*, Cuba), × 6.

FIG. 61. *Phyllanthus pachystylus* Urb. (*Webster 3906*, Cuba); mature carpel, or coccus, showing two seeds in position, × 6. Note the crescent-shaped split in the radial walls of the carpel, and the separation of the two layers of the tangential wall. FIG. 62. Seeds, × 6.

FIG. 63. *Phyllanthus nutans* Sw. (*Britton 929*, Jamaica [NY]), × 6.

FIG. 64. *Phyllanthus juglandifolius* Willd. (*Webster 4028*, Cuba), × 6.

FIG. 65. *Phyllanthus ekmanii* Webster (*Ekman 6206*, Cuba [S]), × 6.

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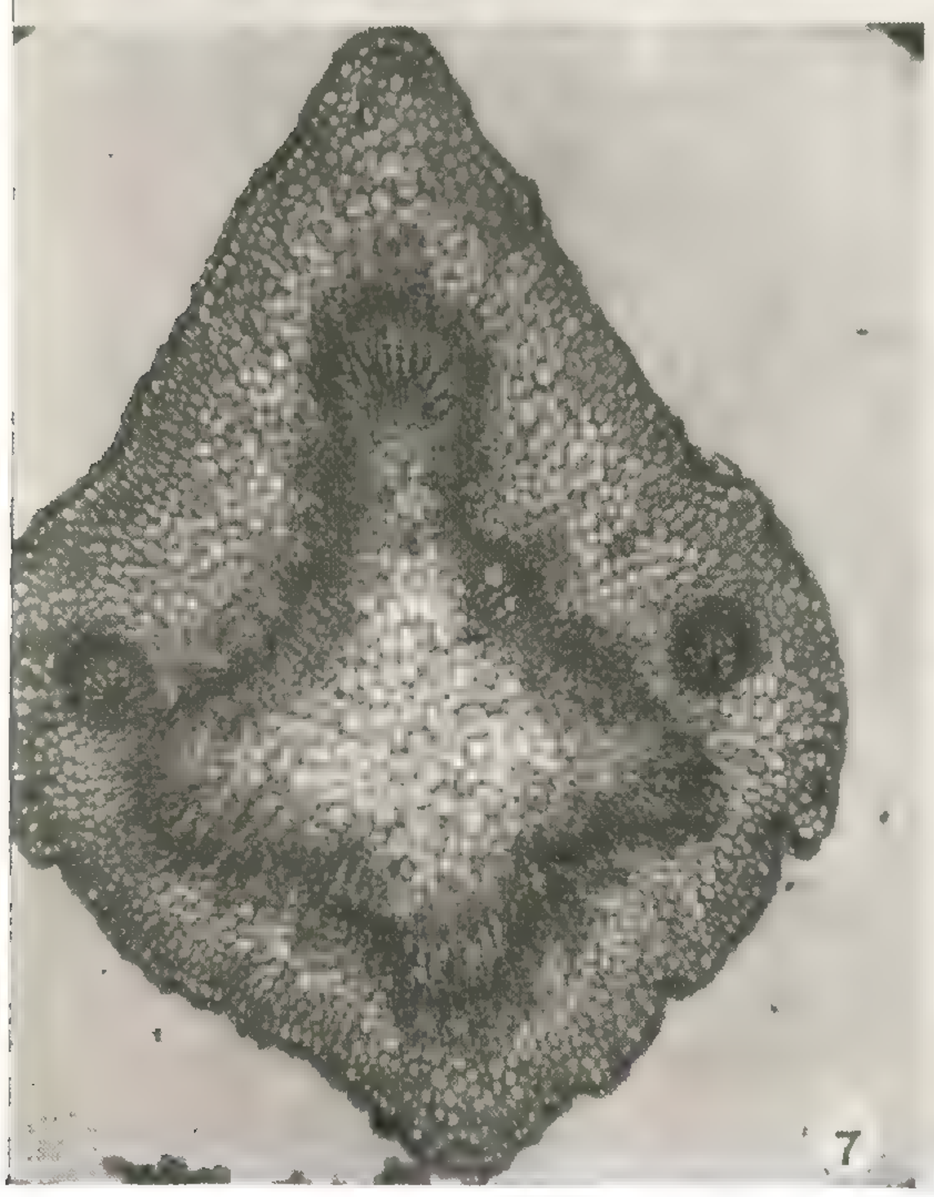

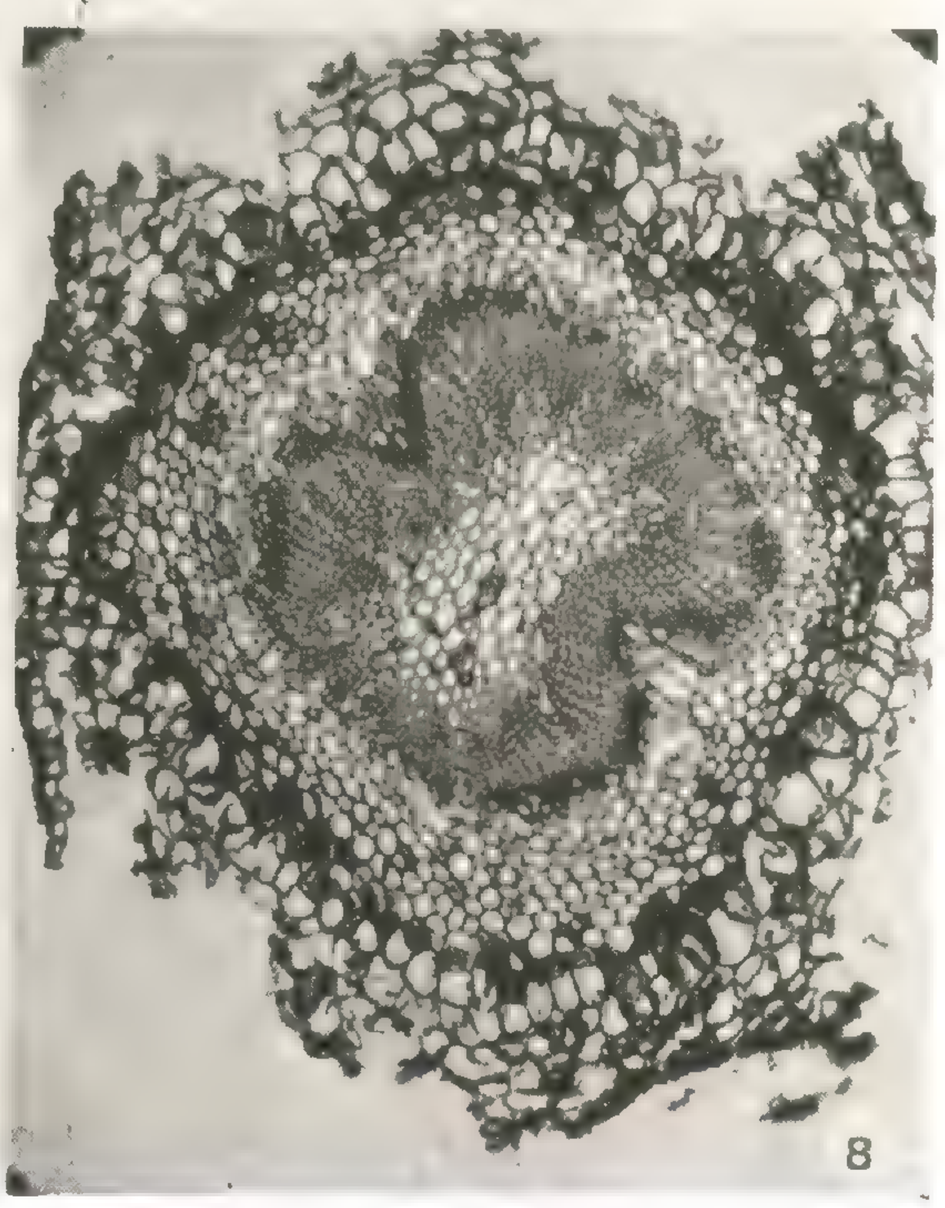

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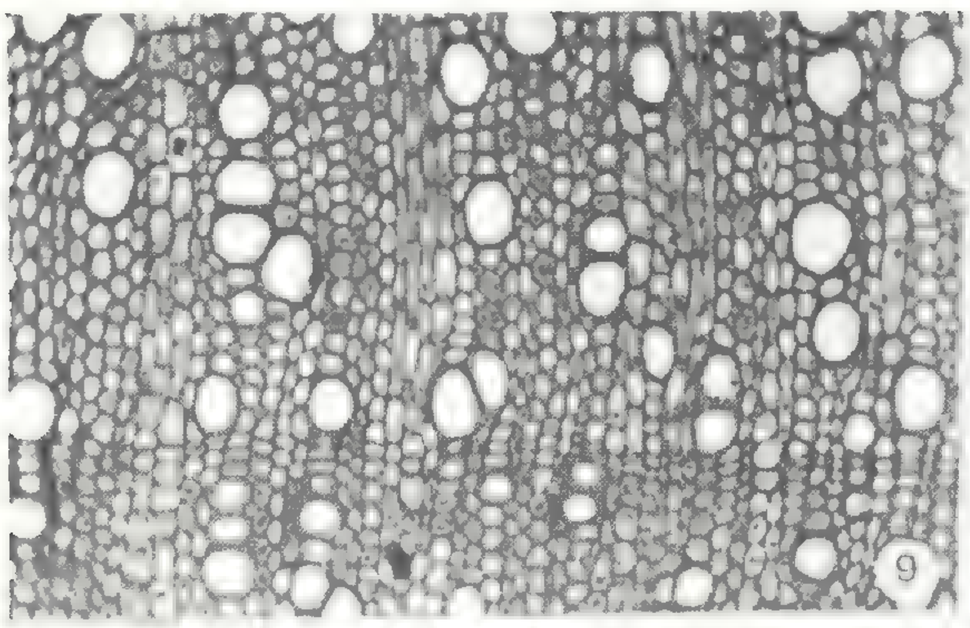
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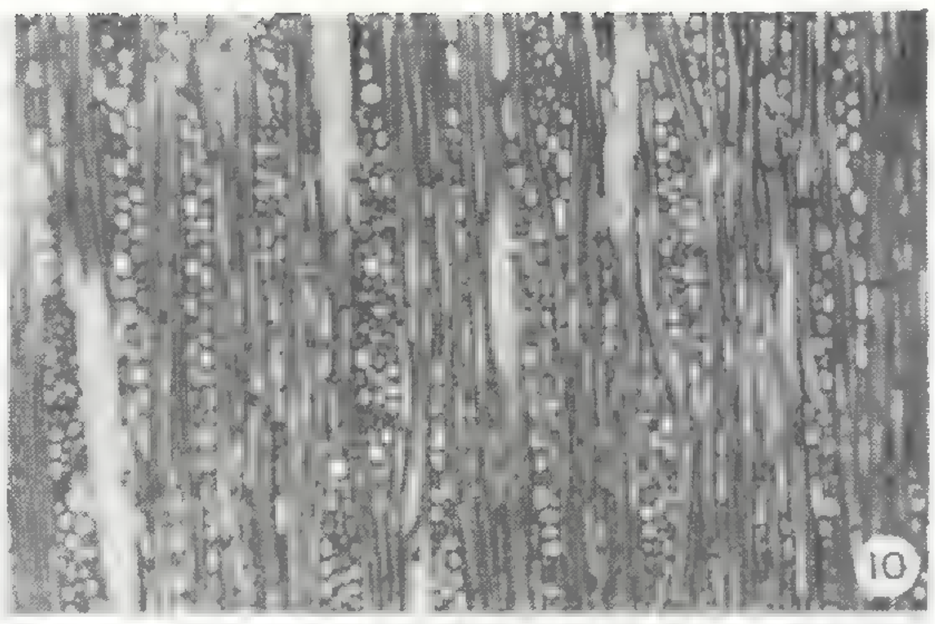
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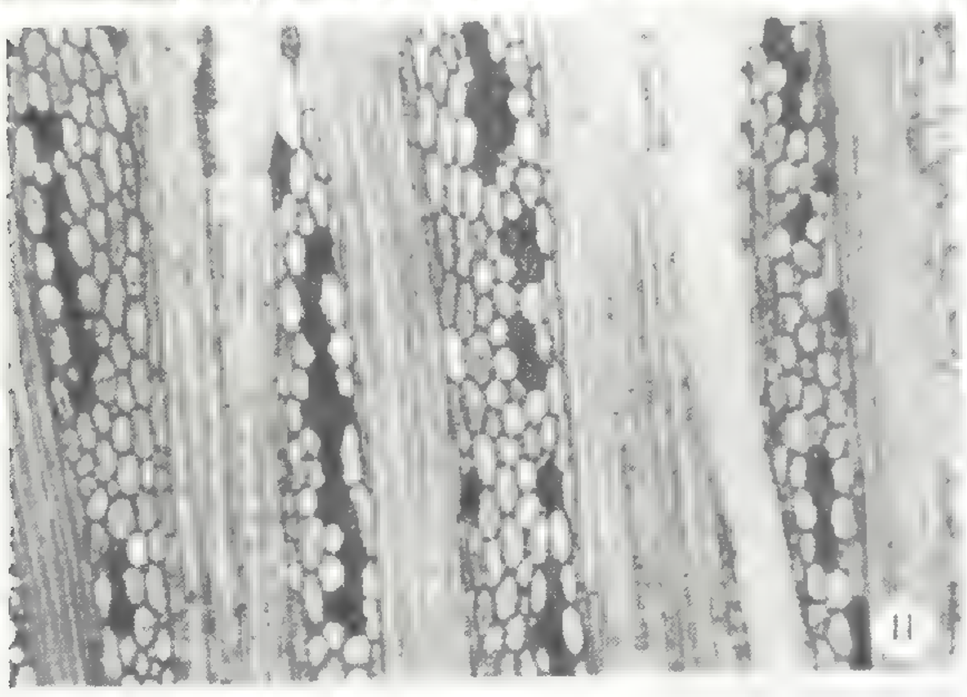
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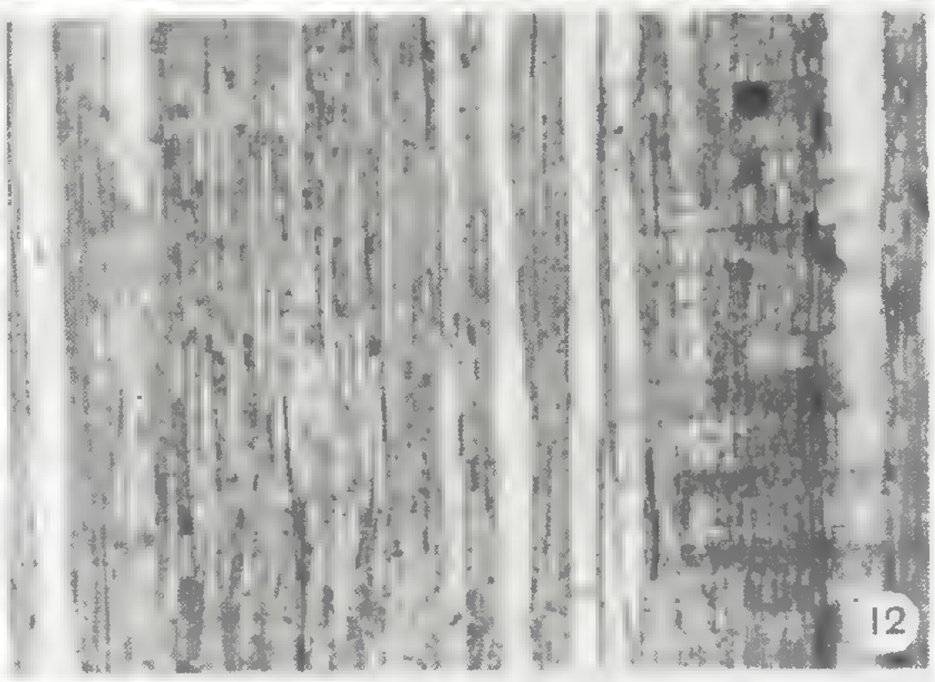
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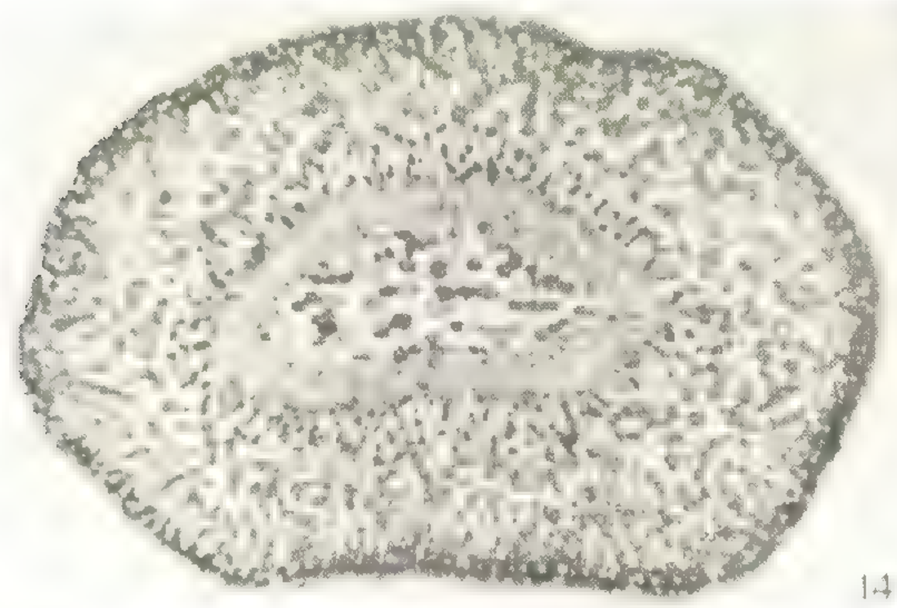

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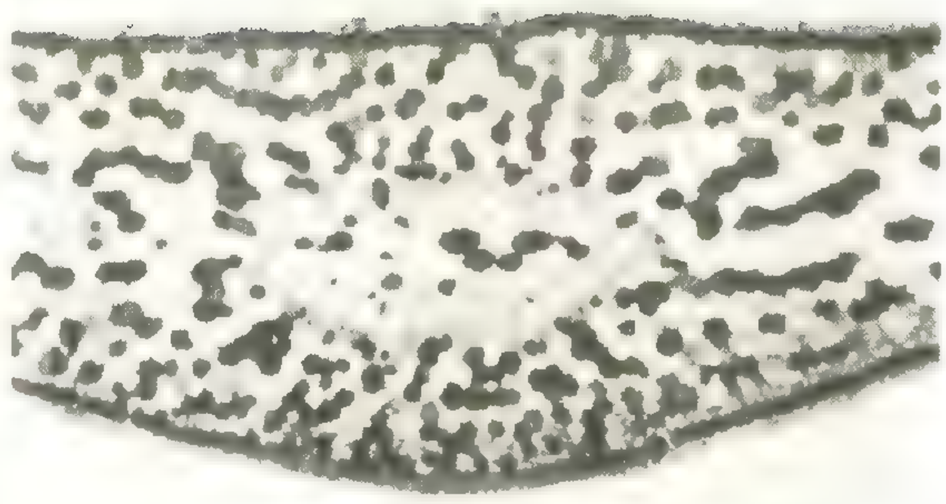

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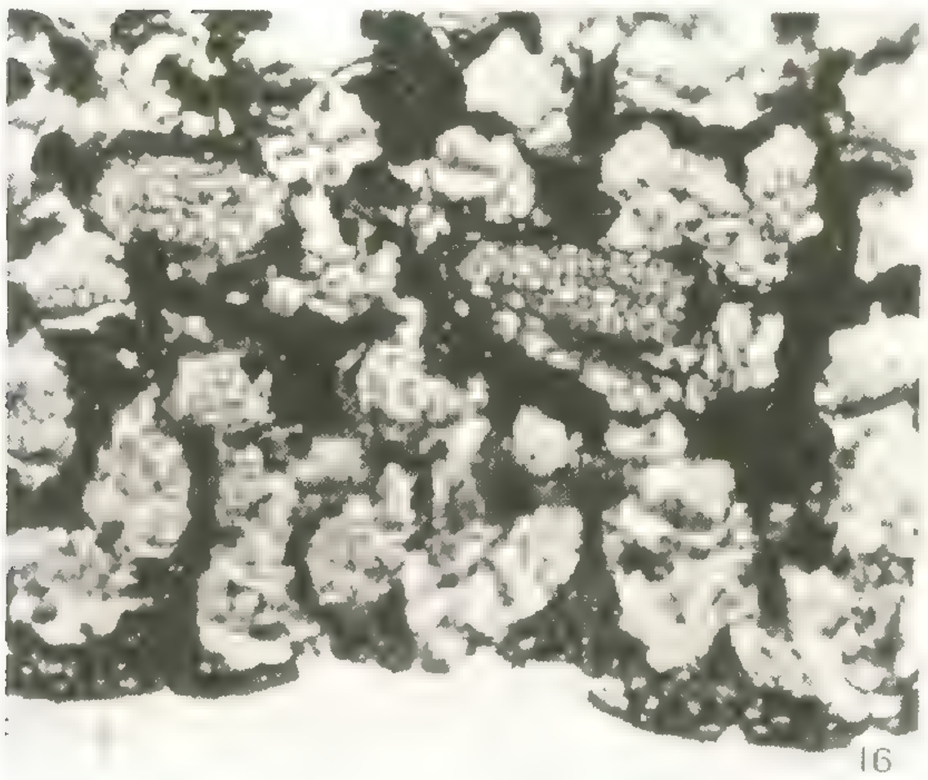

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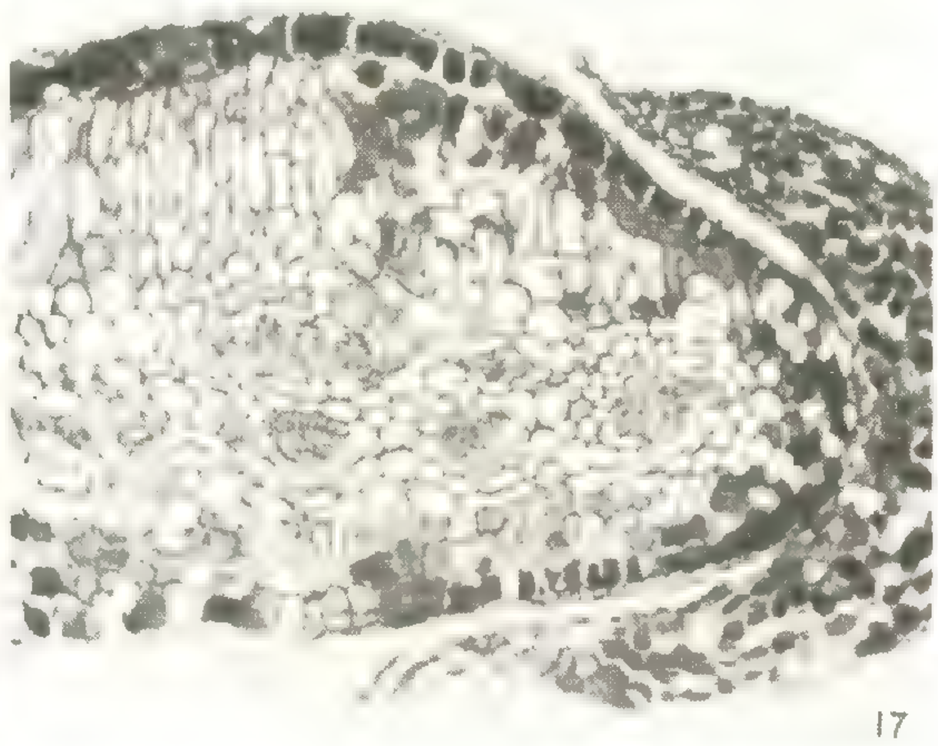

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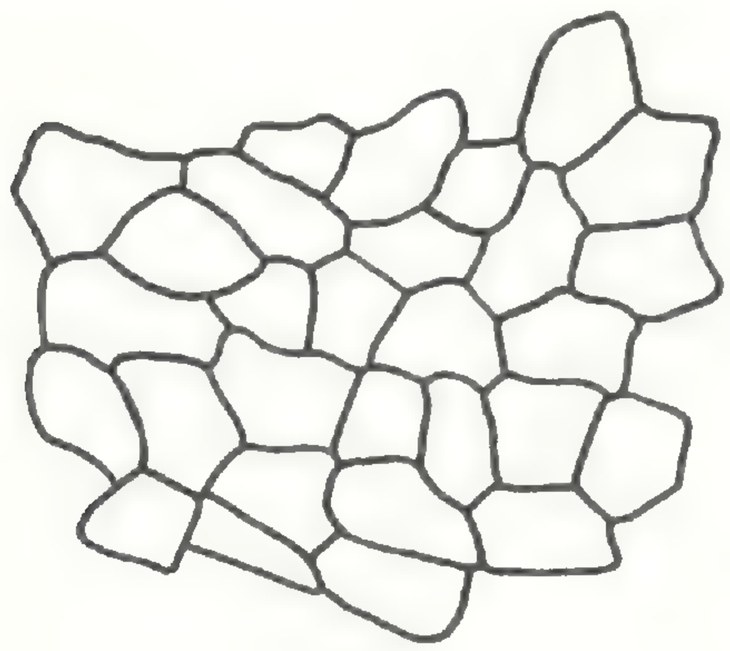

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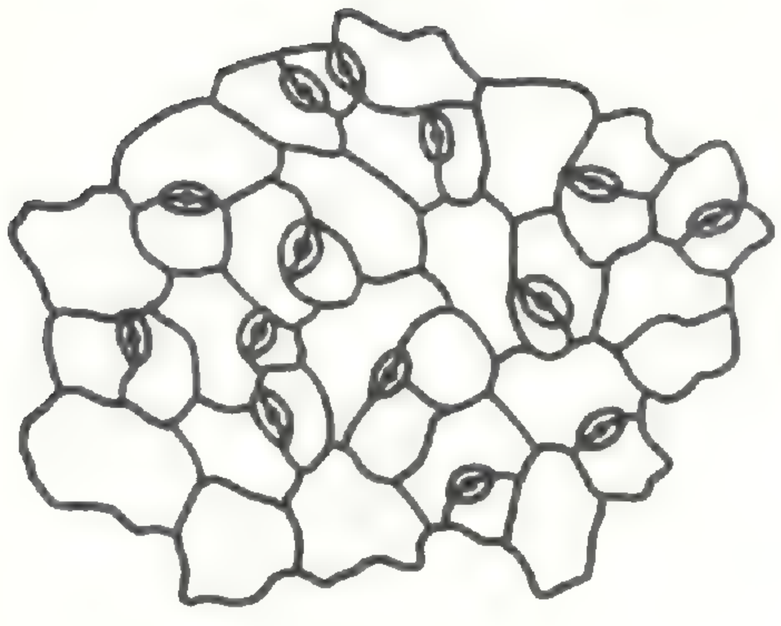

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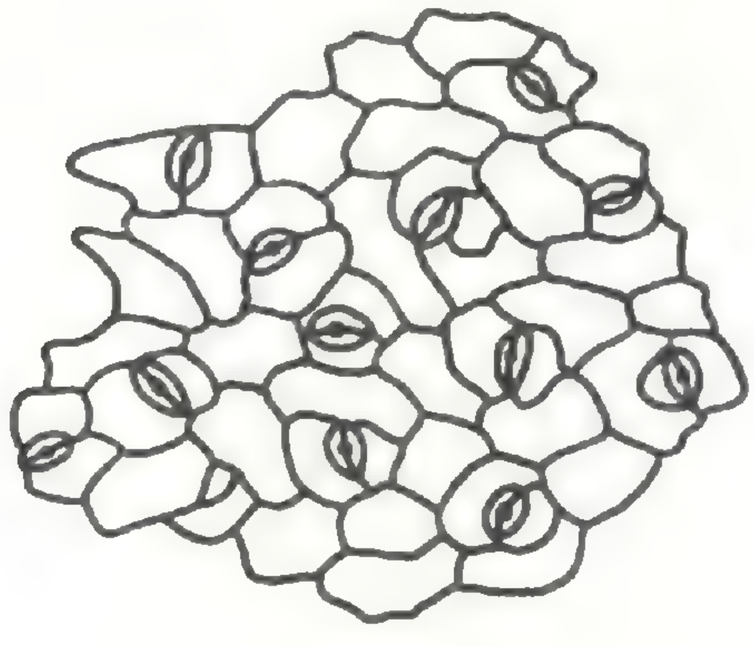

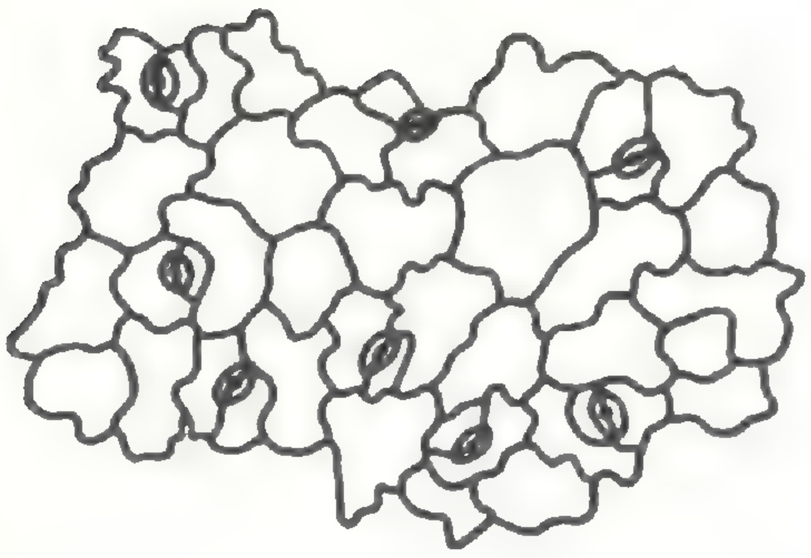

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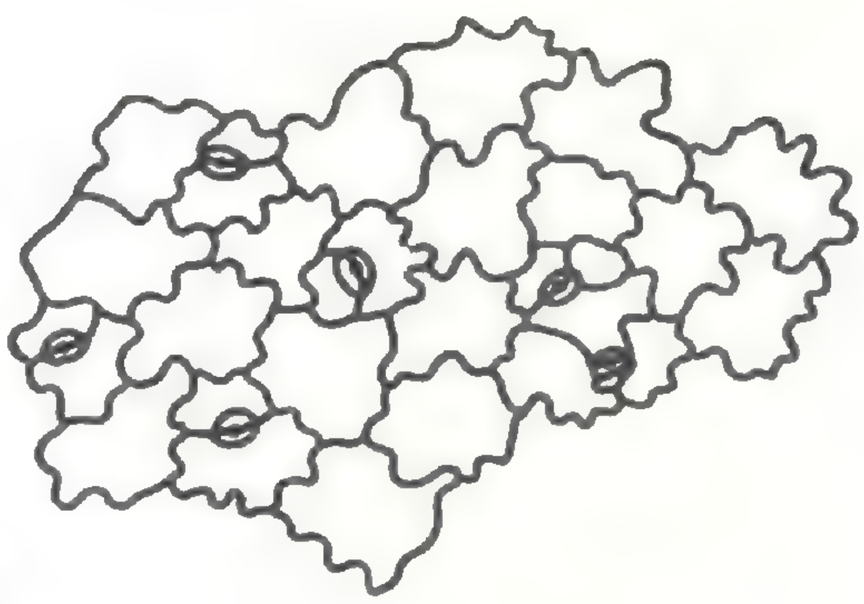

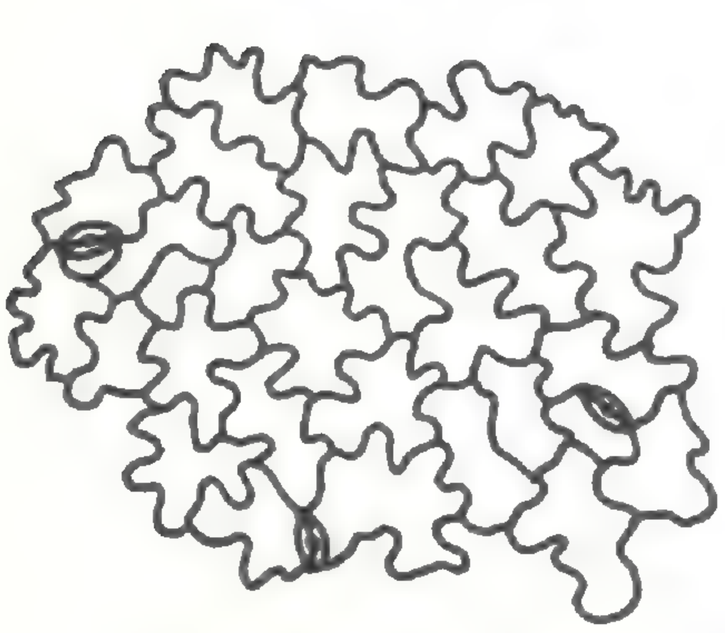

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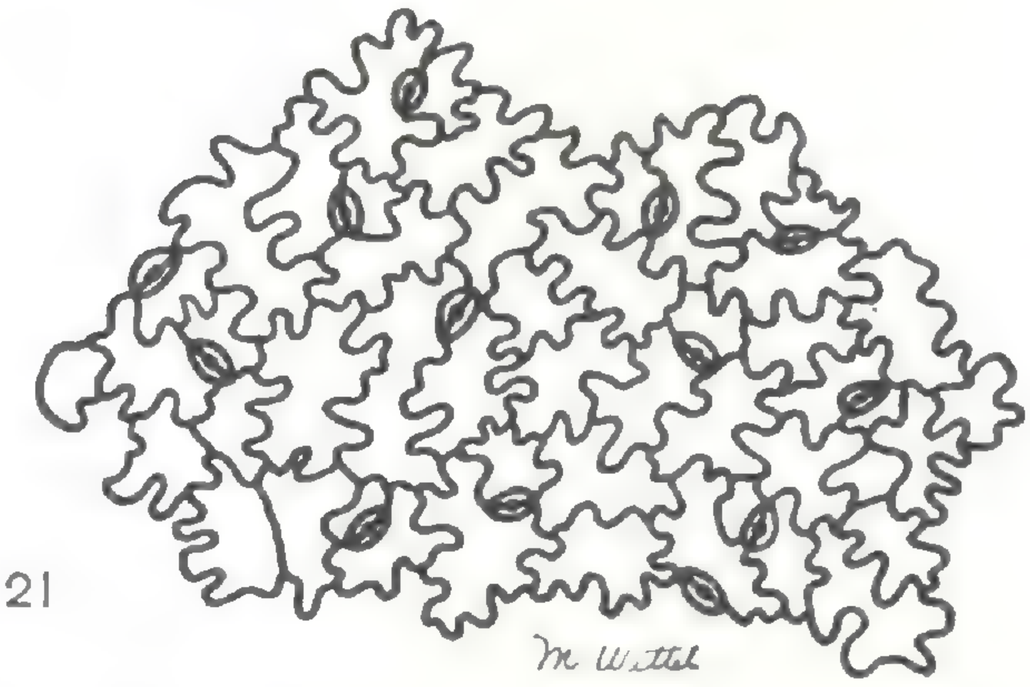

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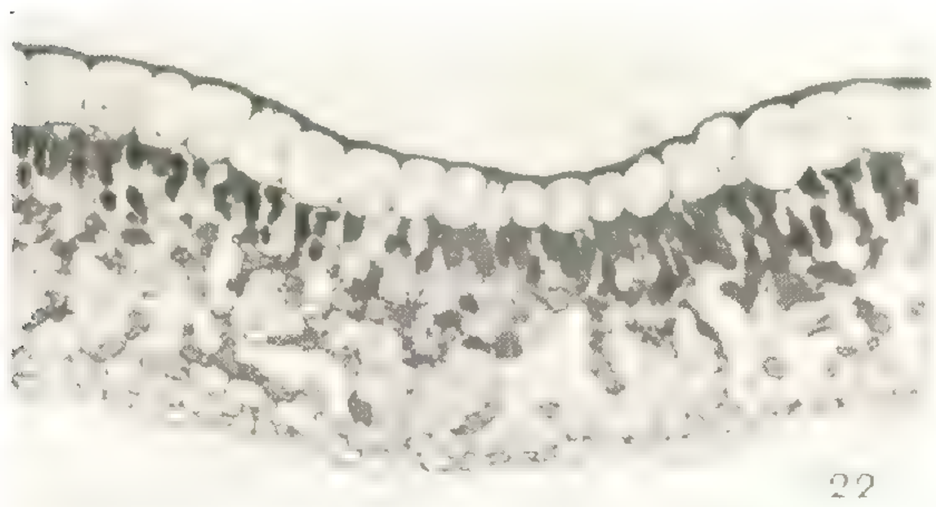

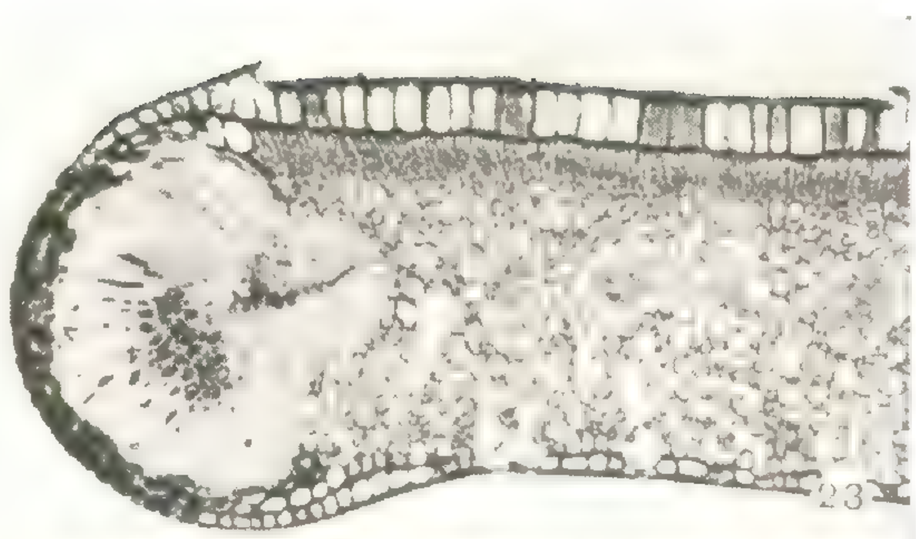

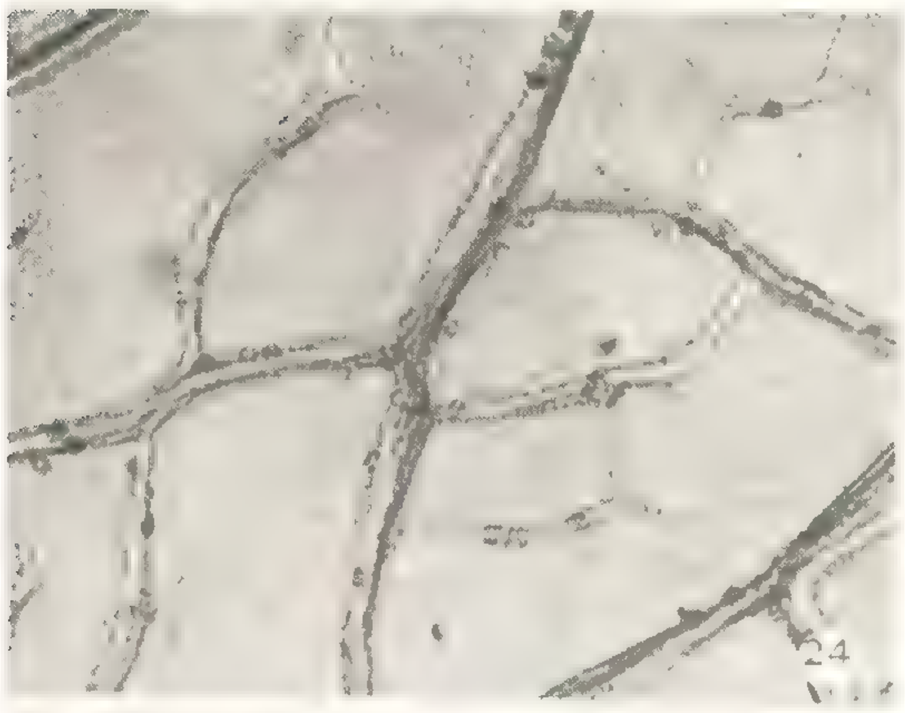

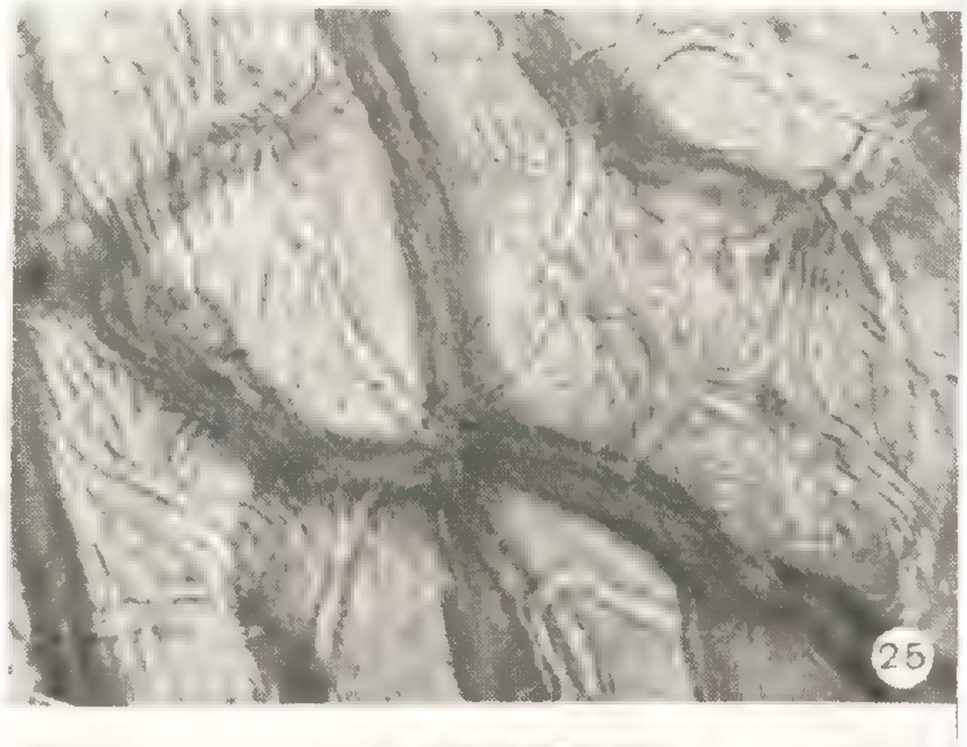

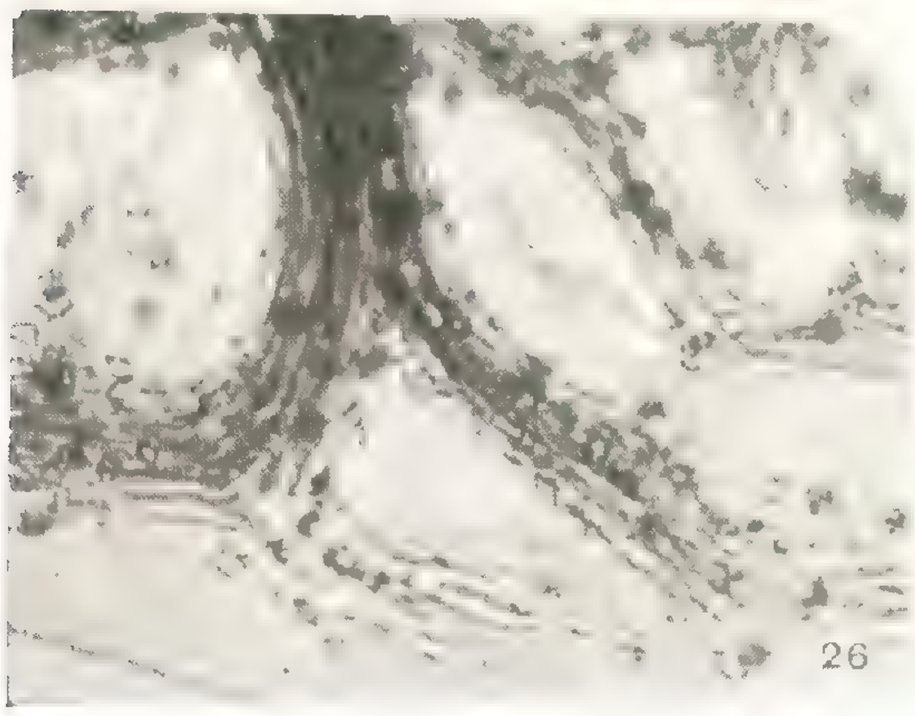

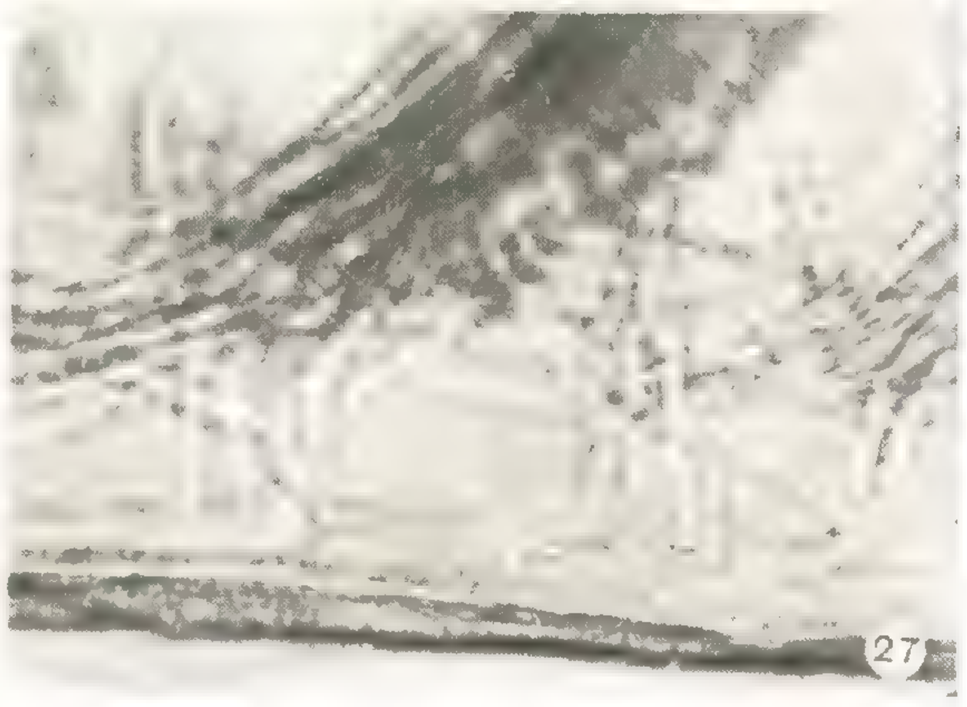

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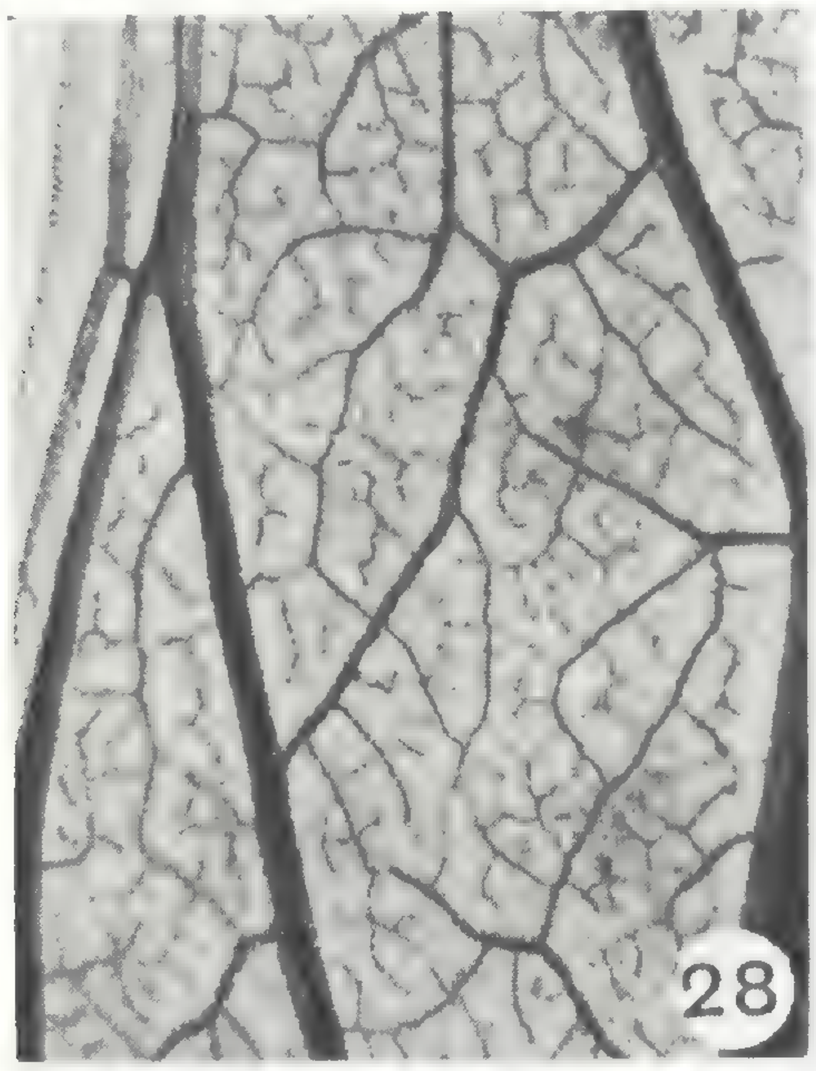

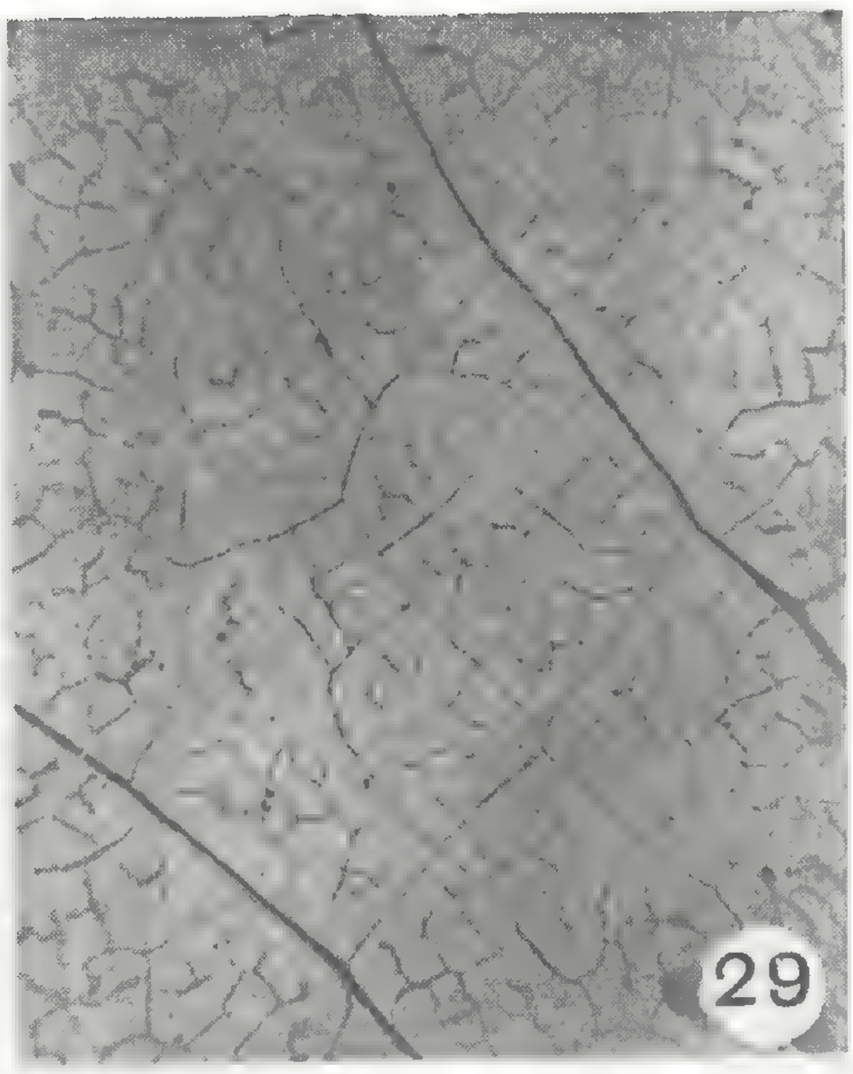

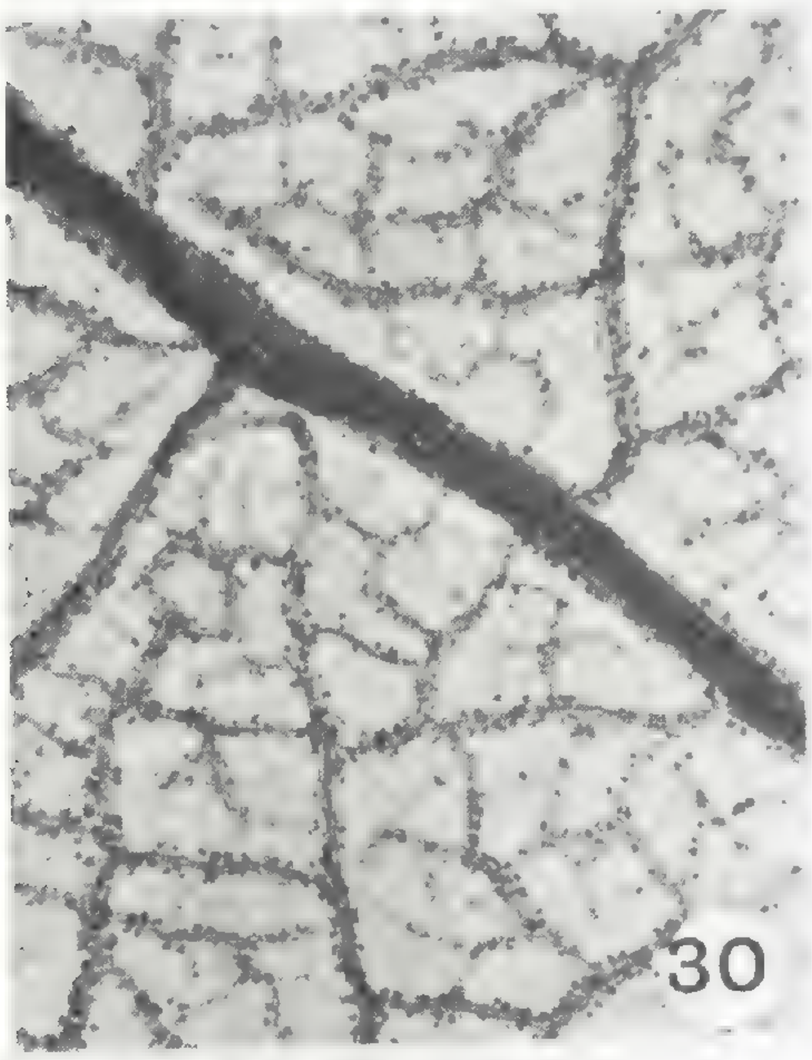

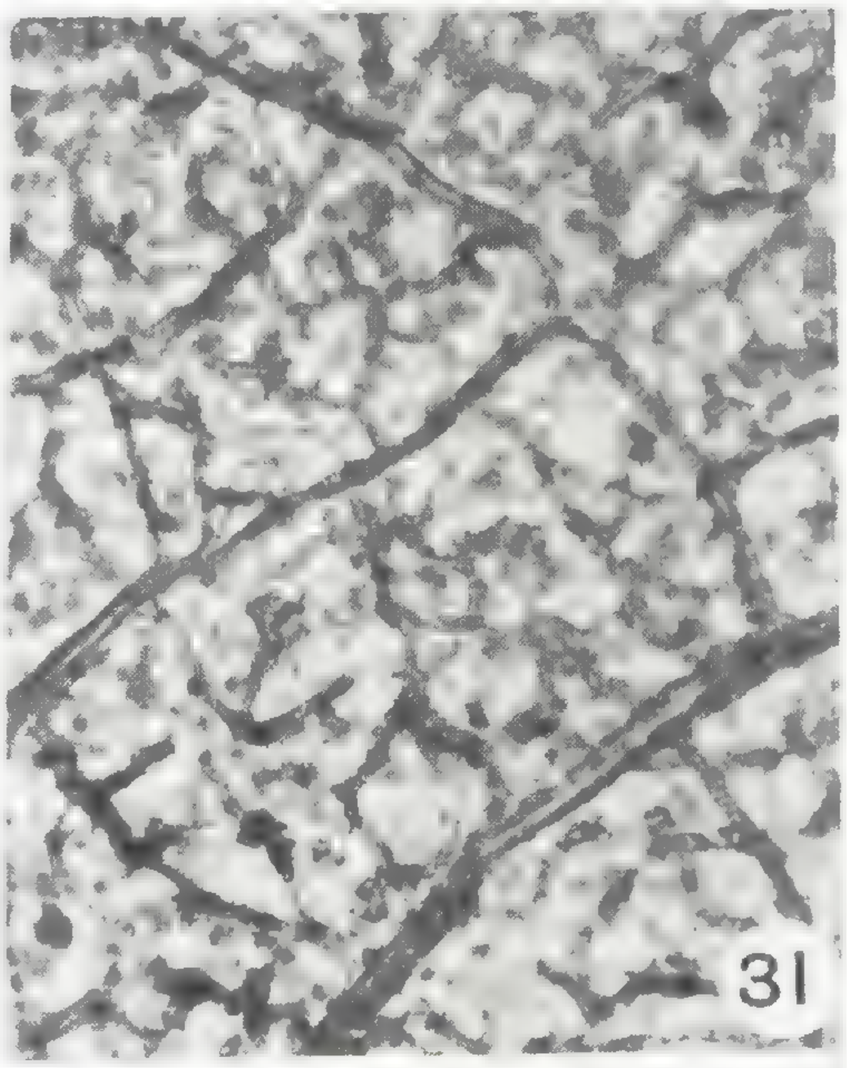

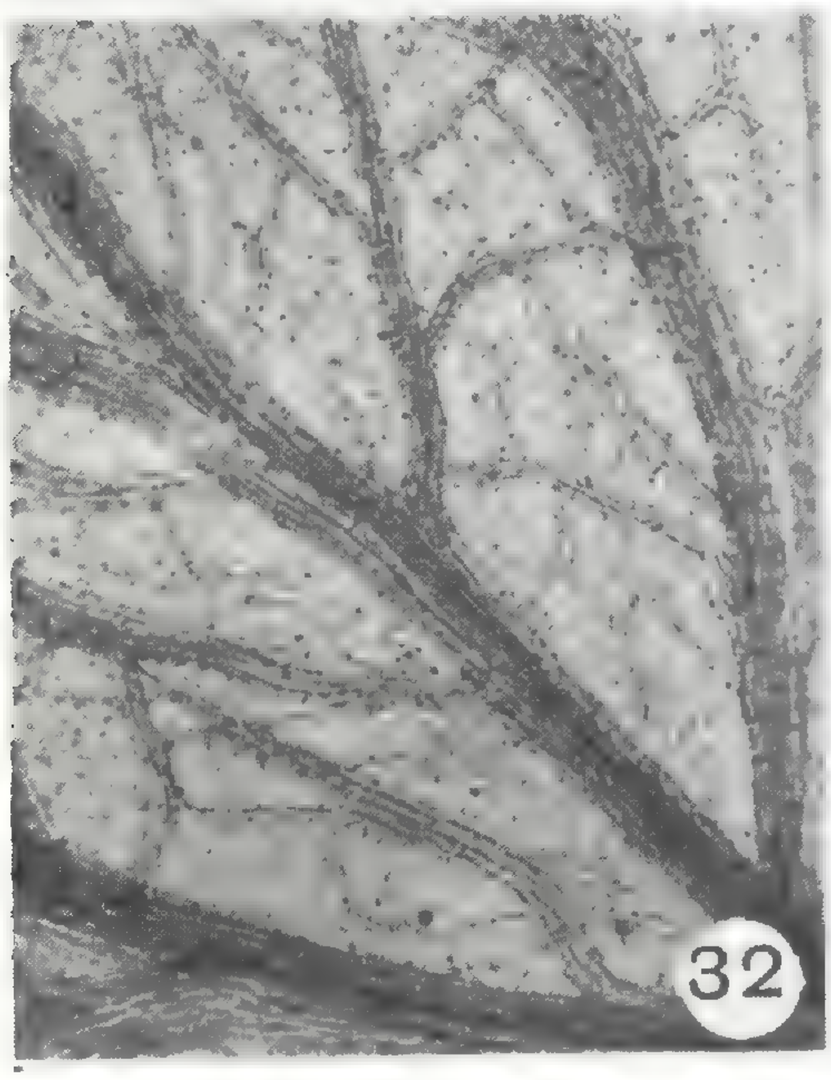

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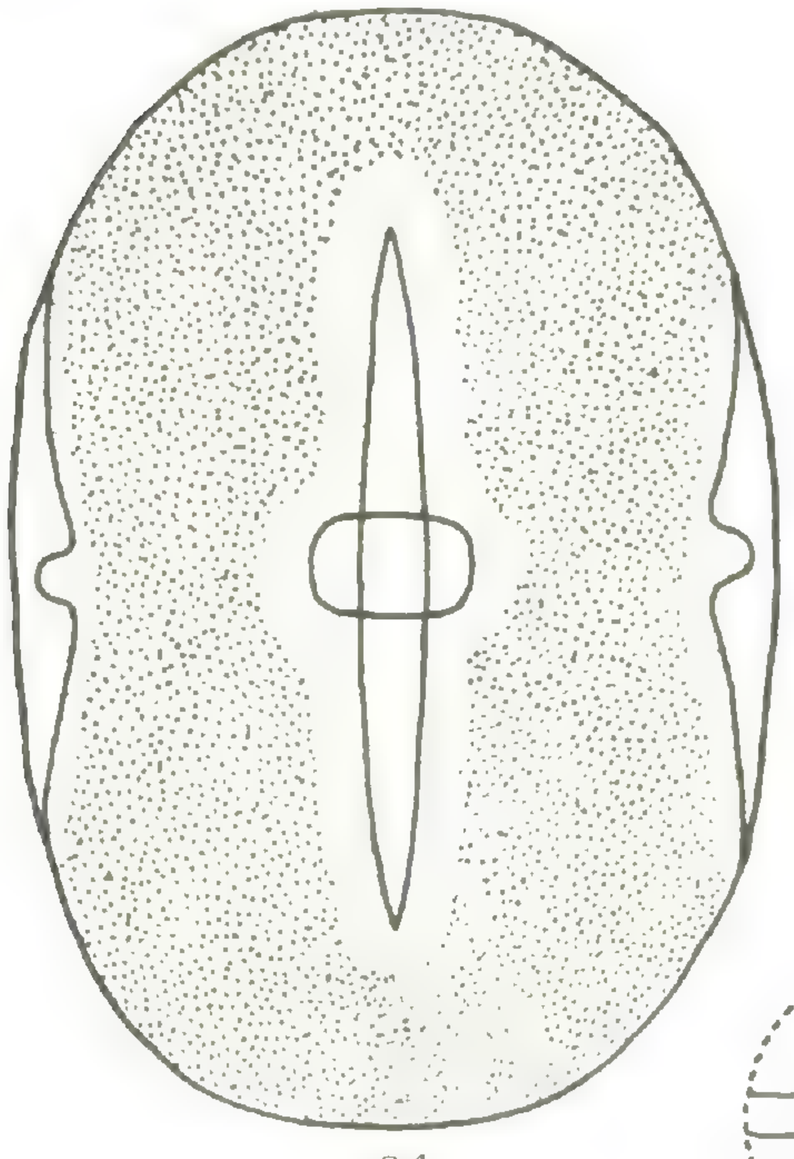

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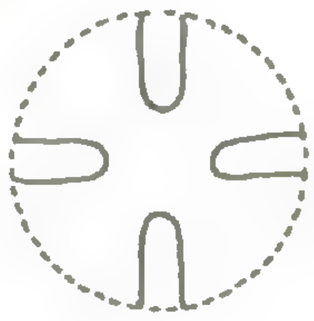

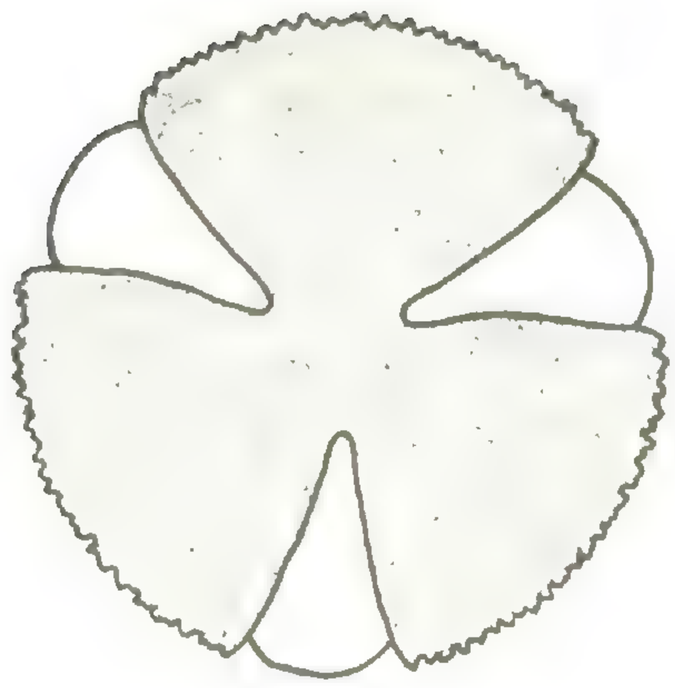

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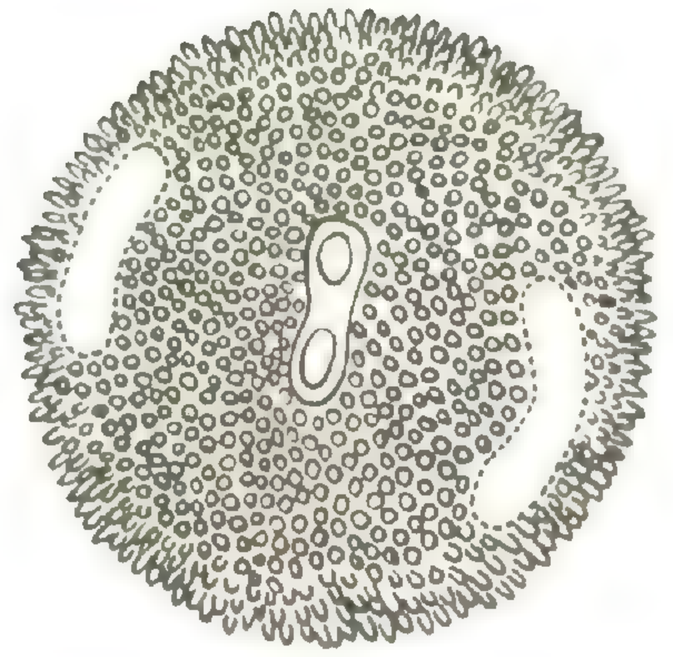

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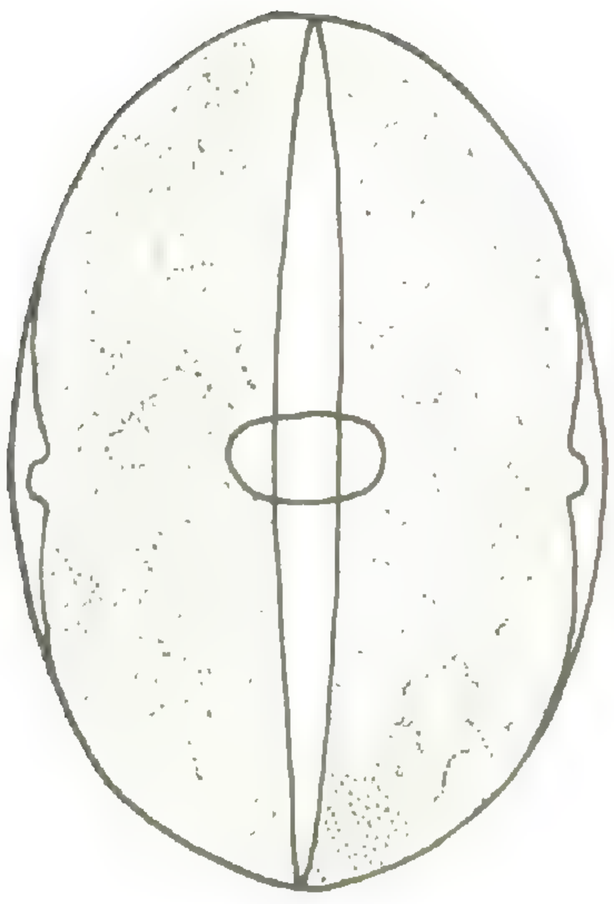

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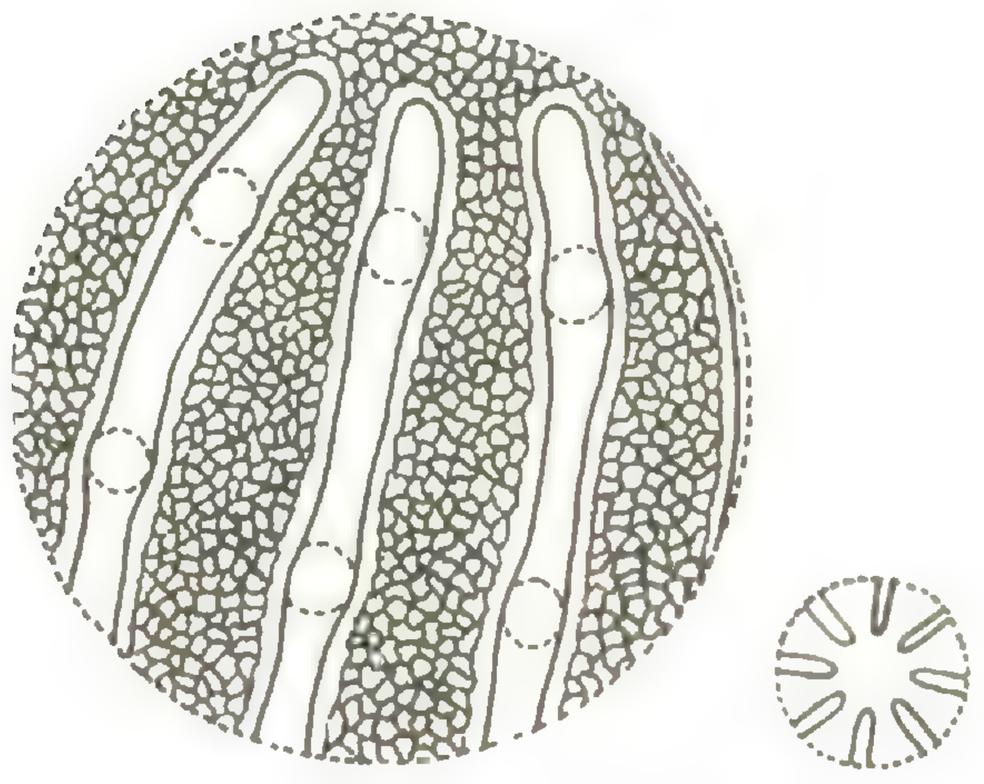

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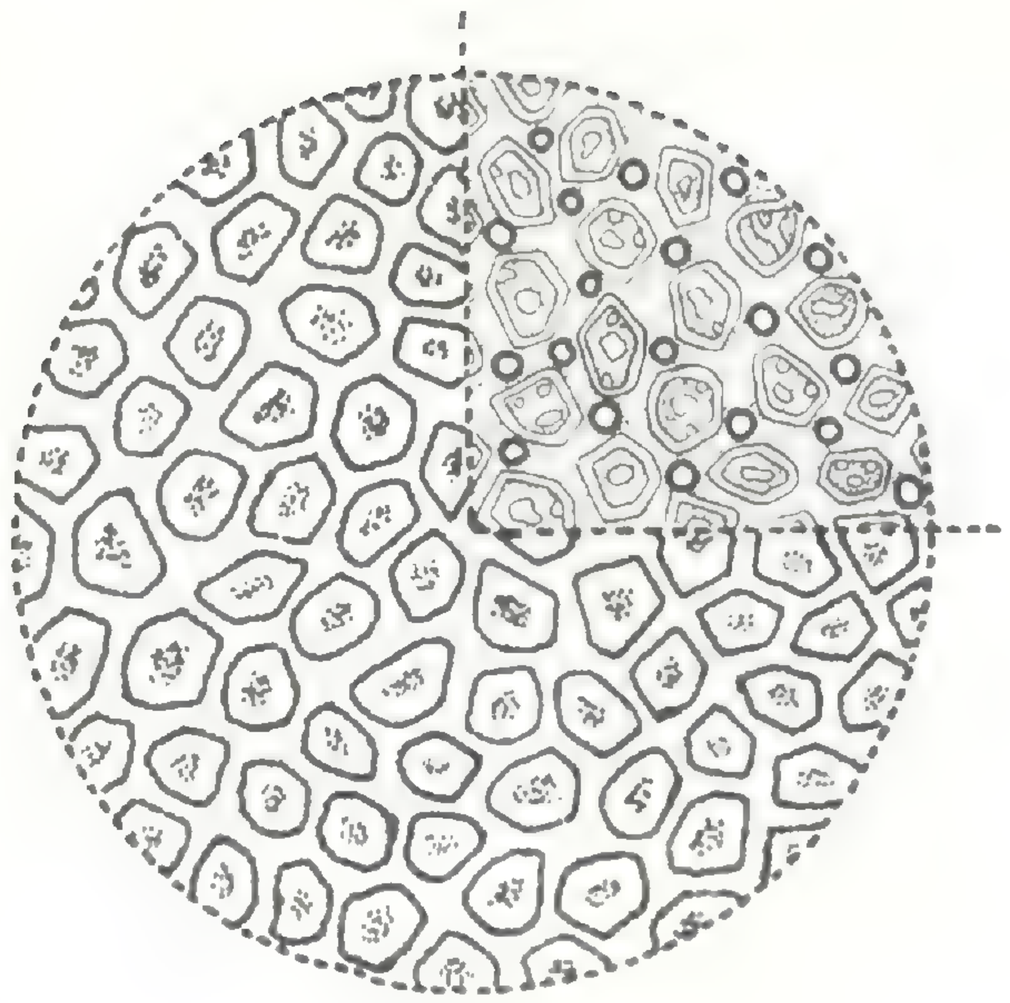

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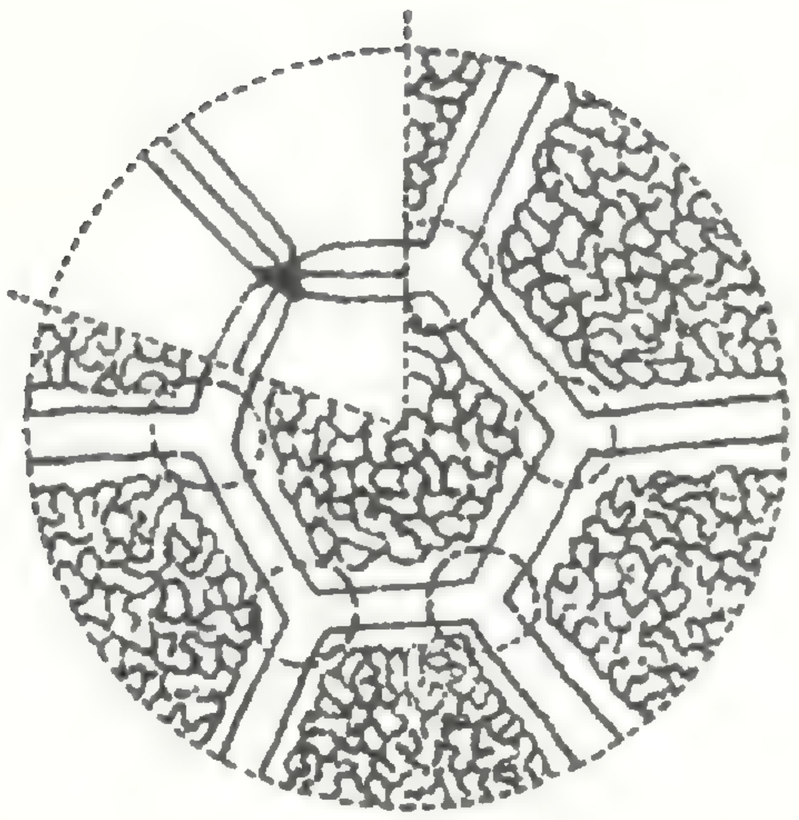

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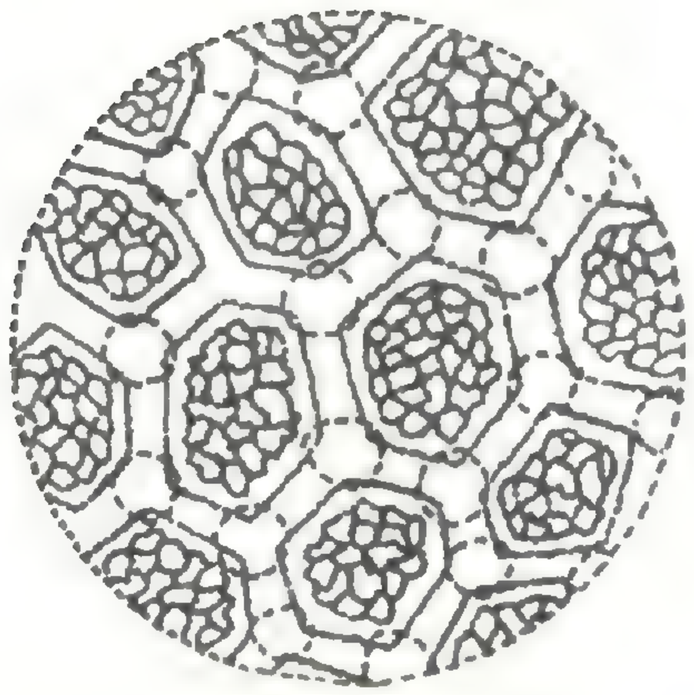

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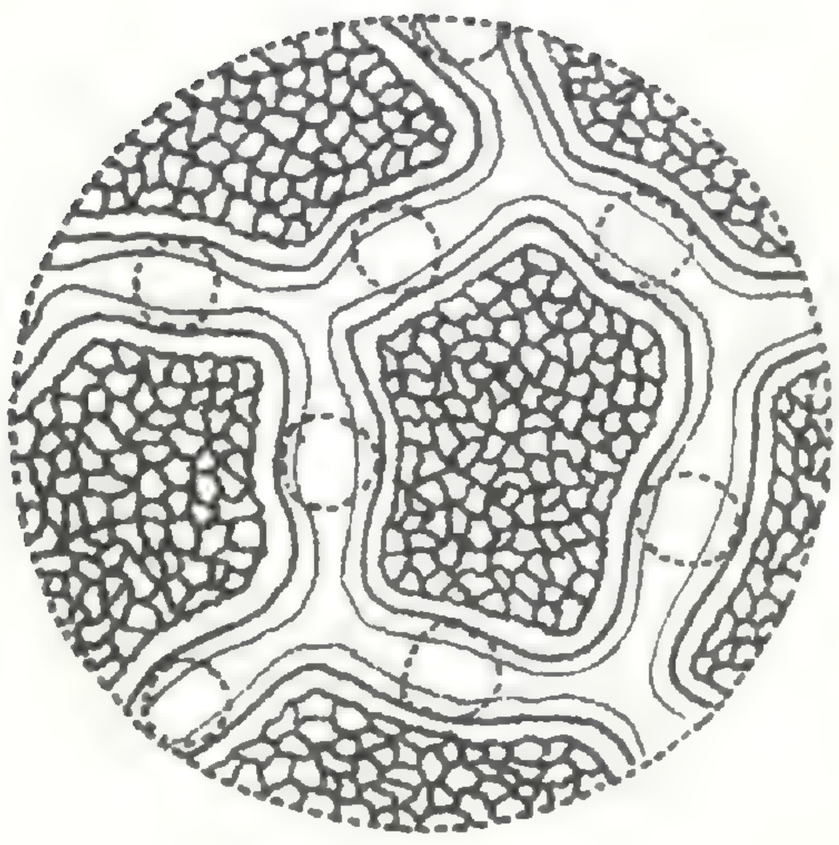

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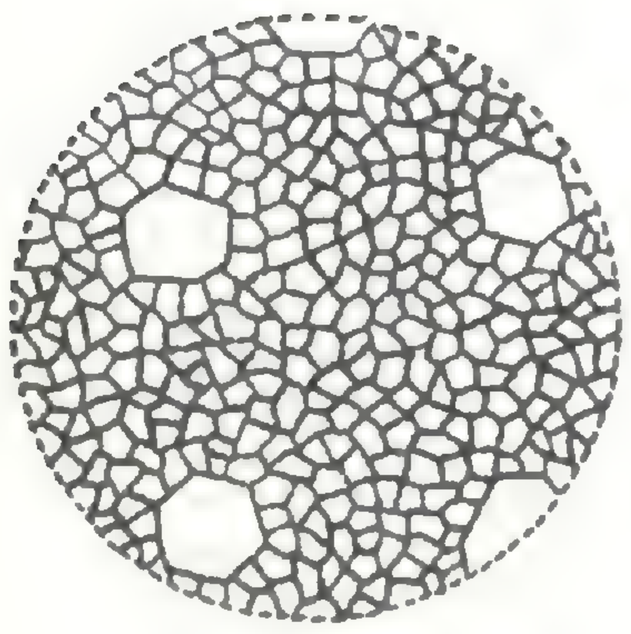

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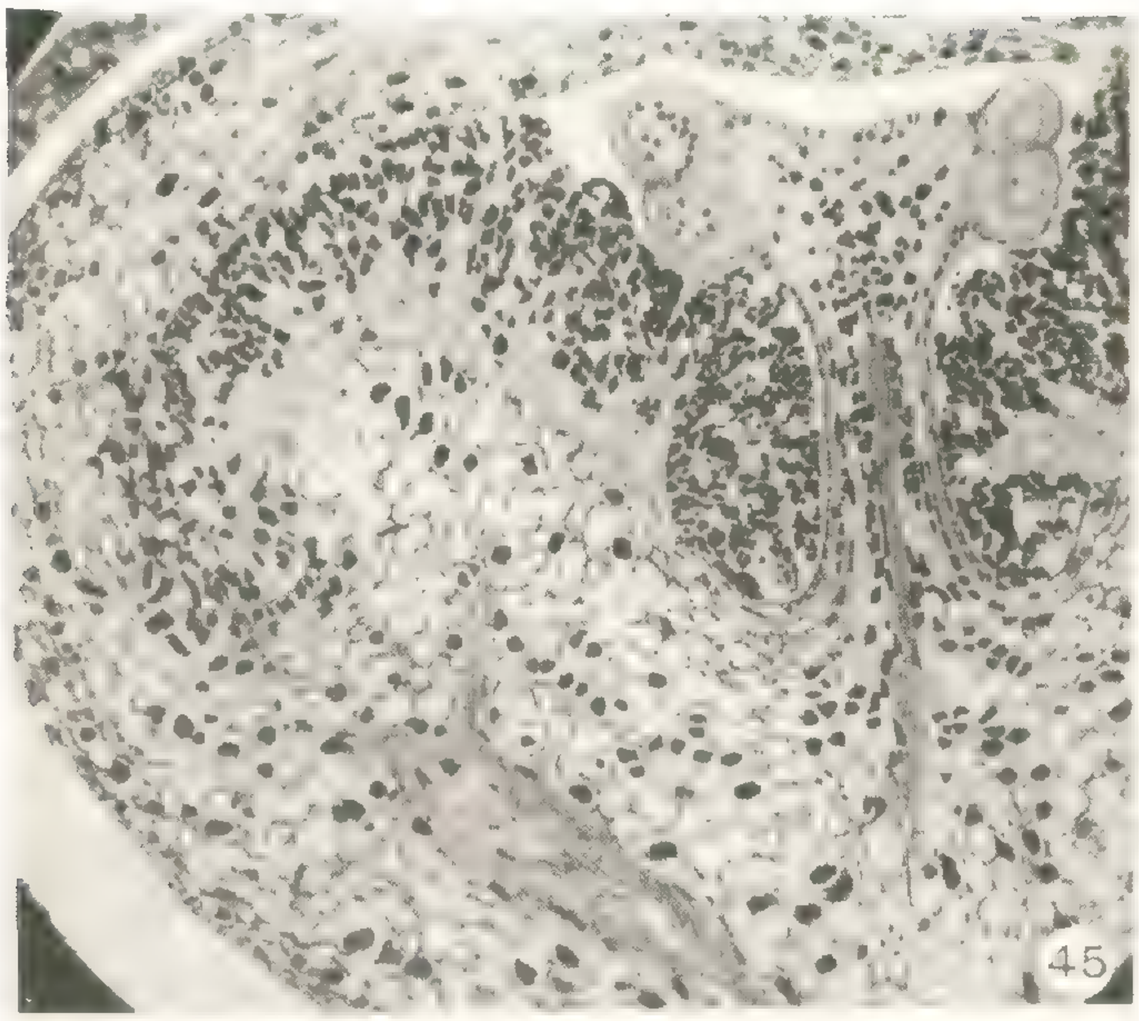
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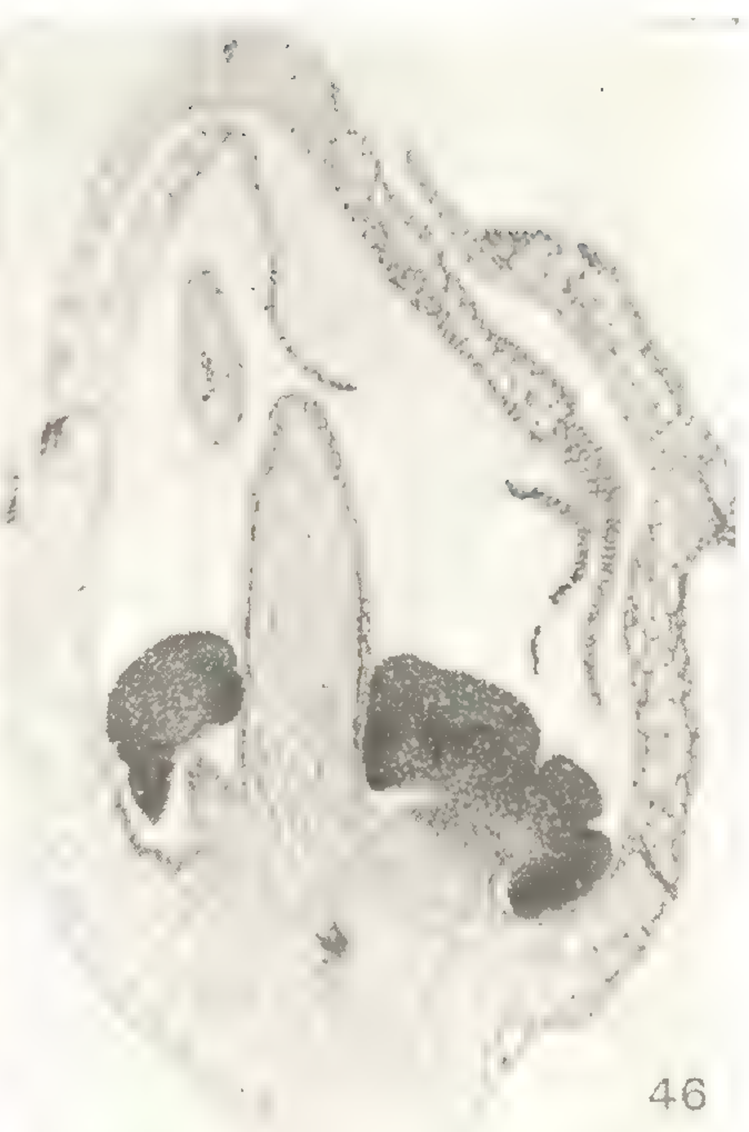
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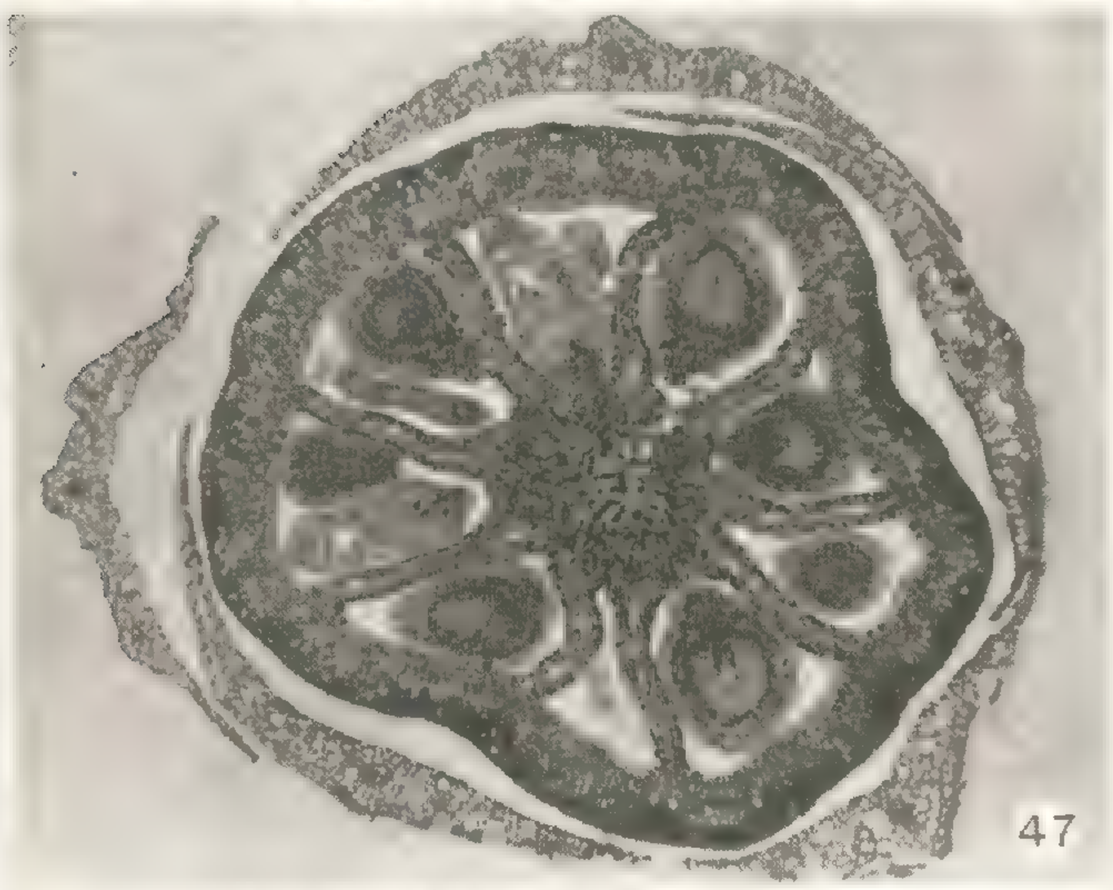
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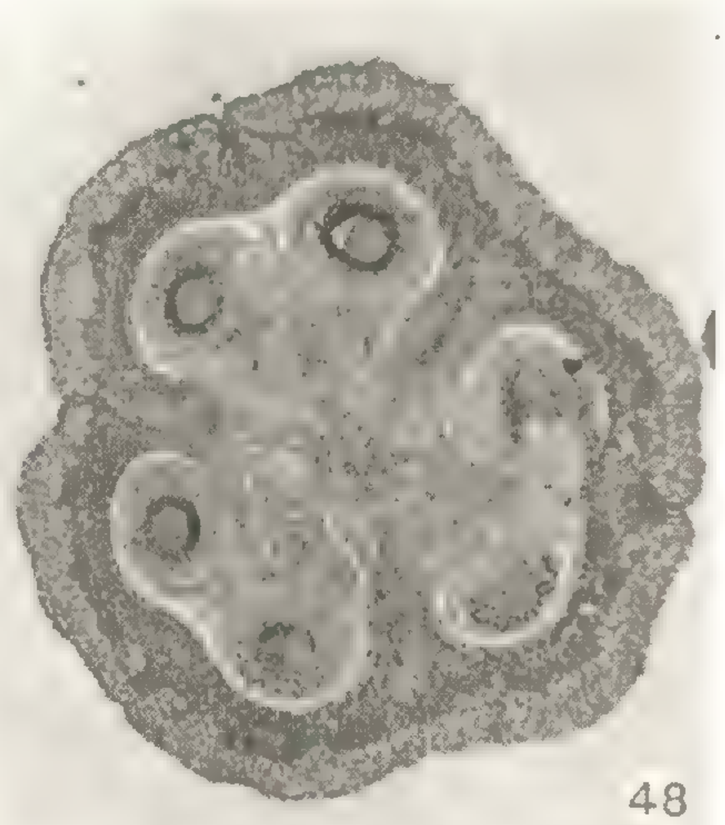
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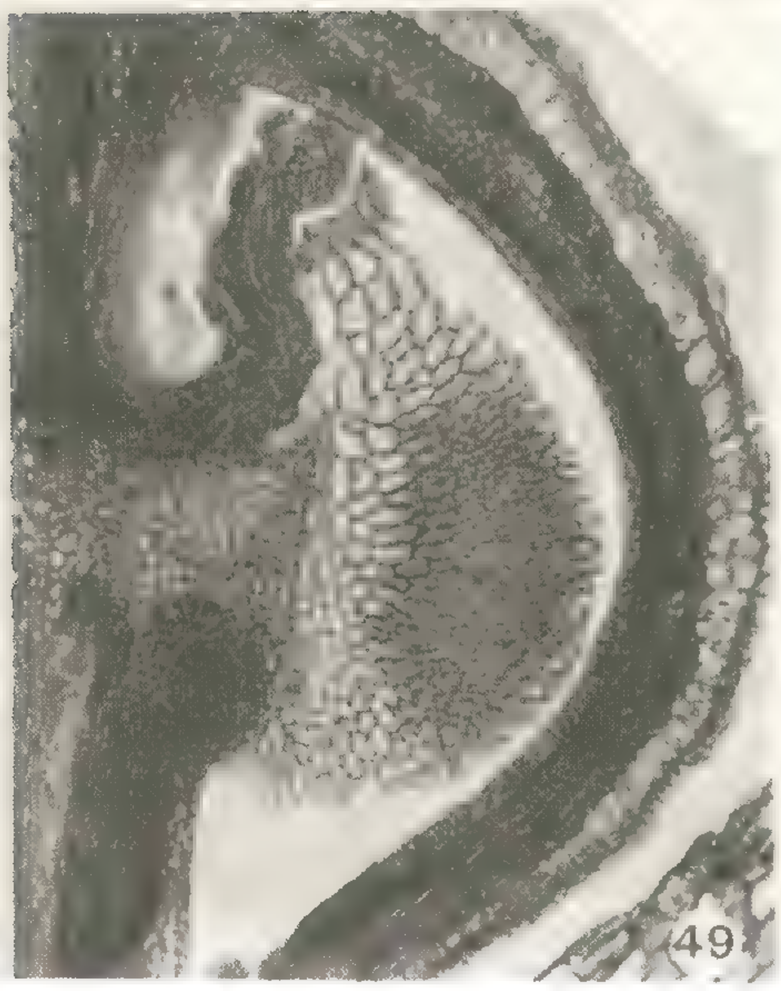
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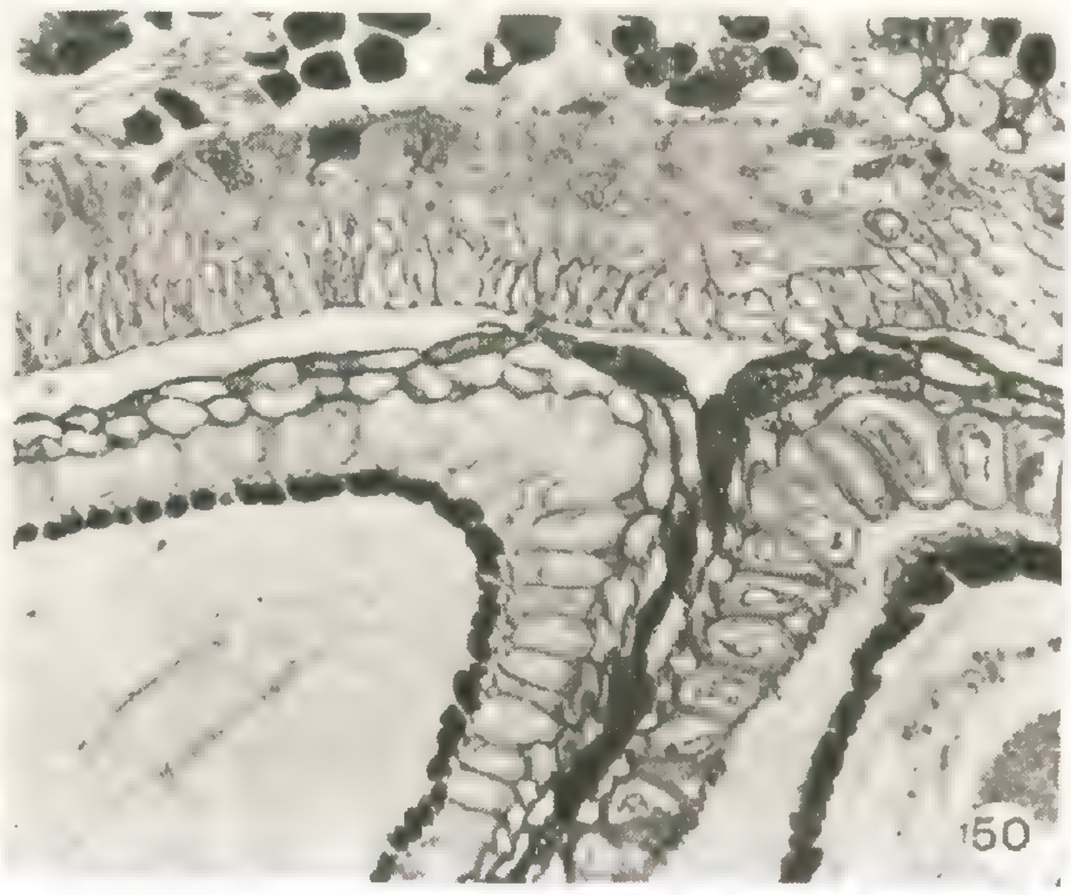
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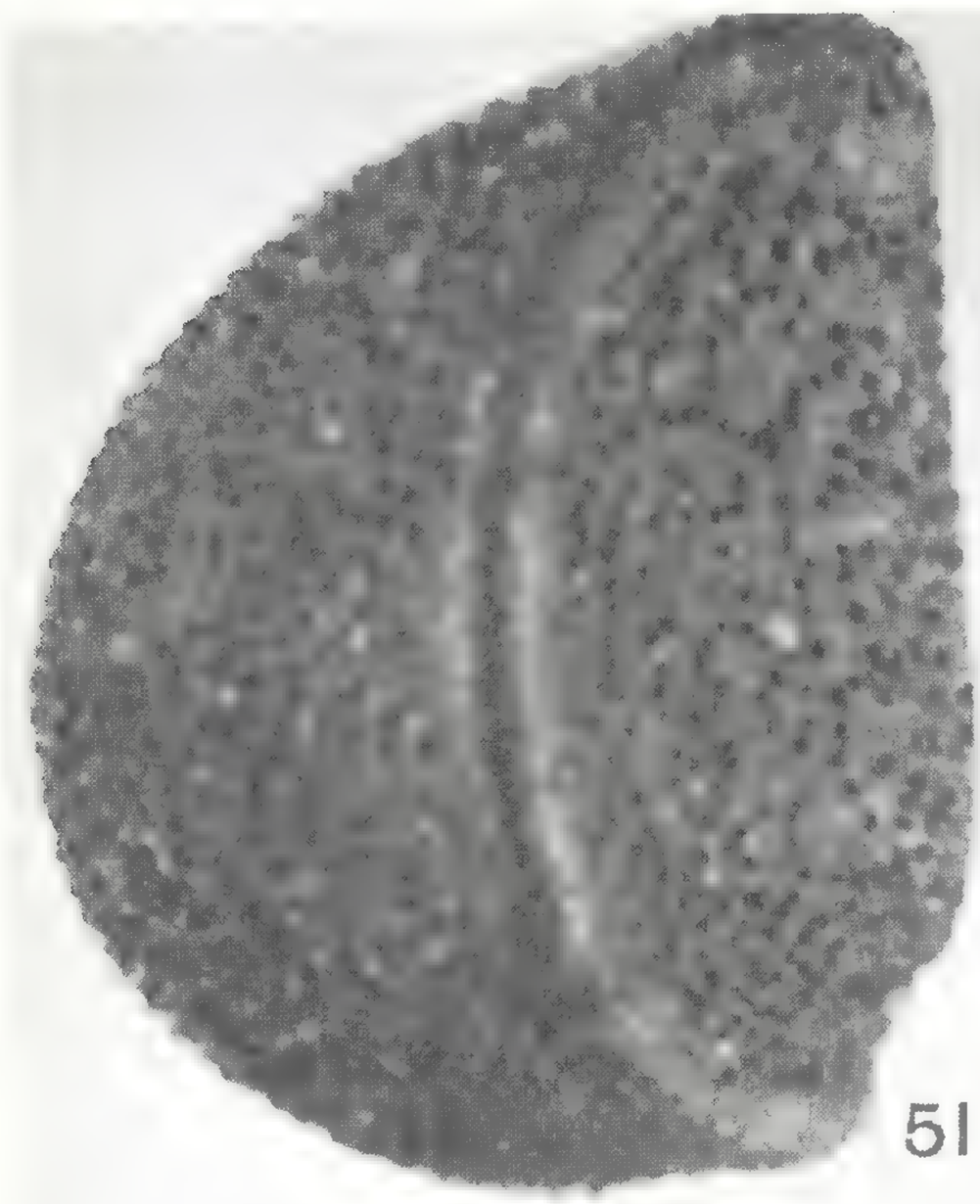

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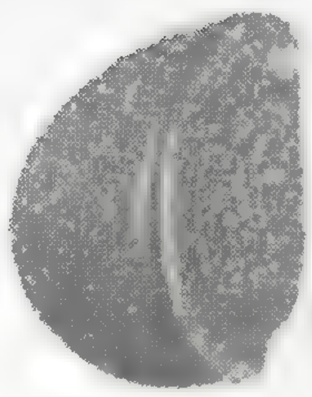

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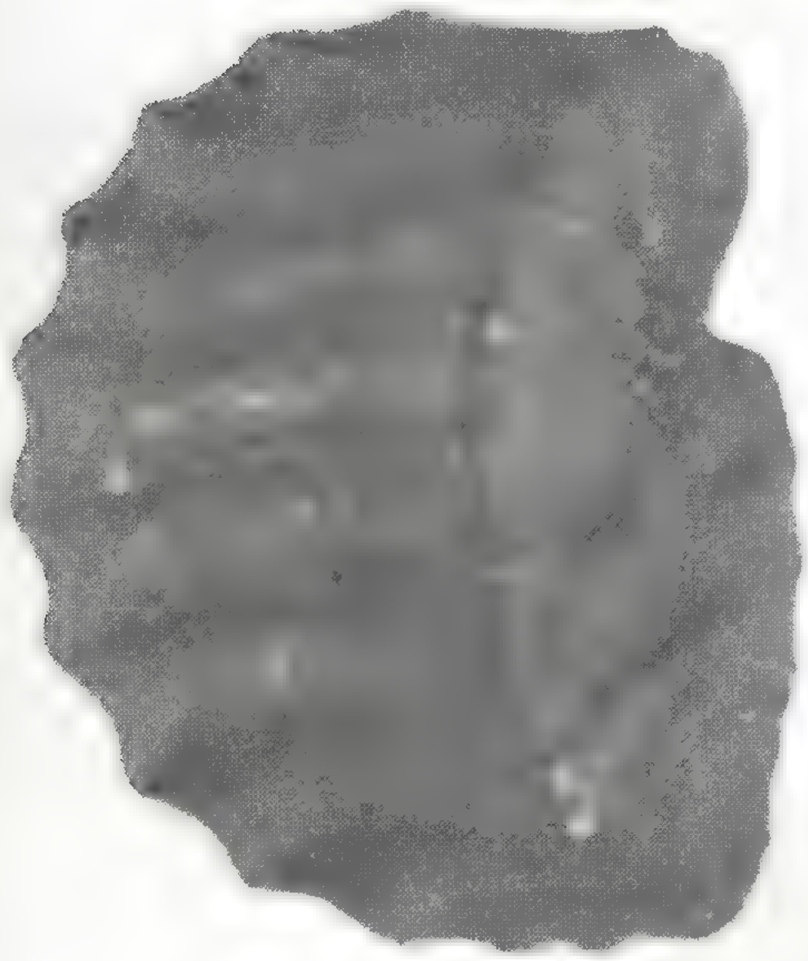

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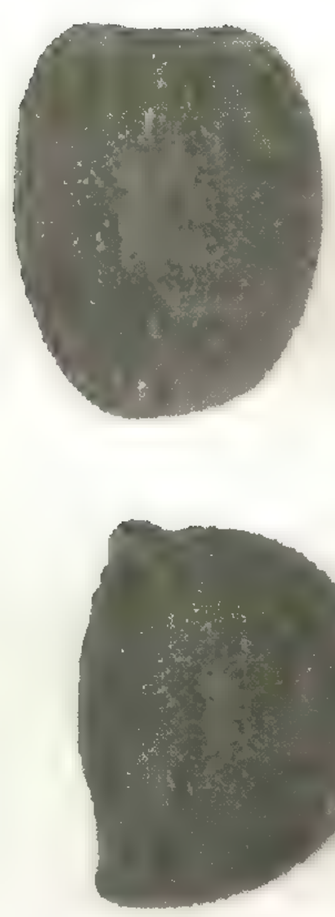

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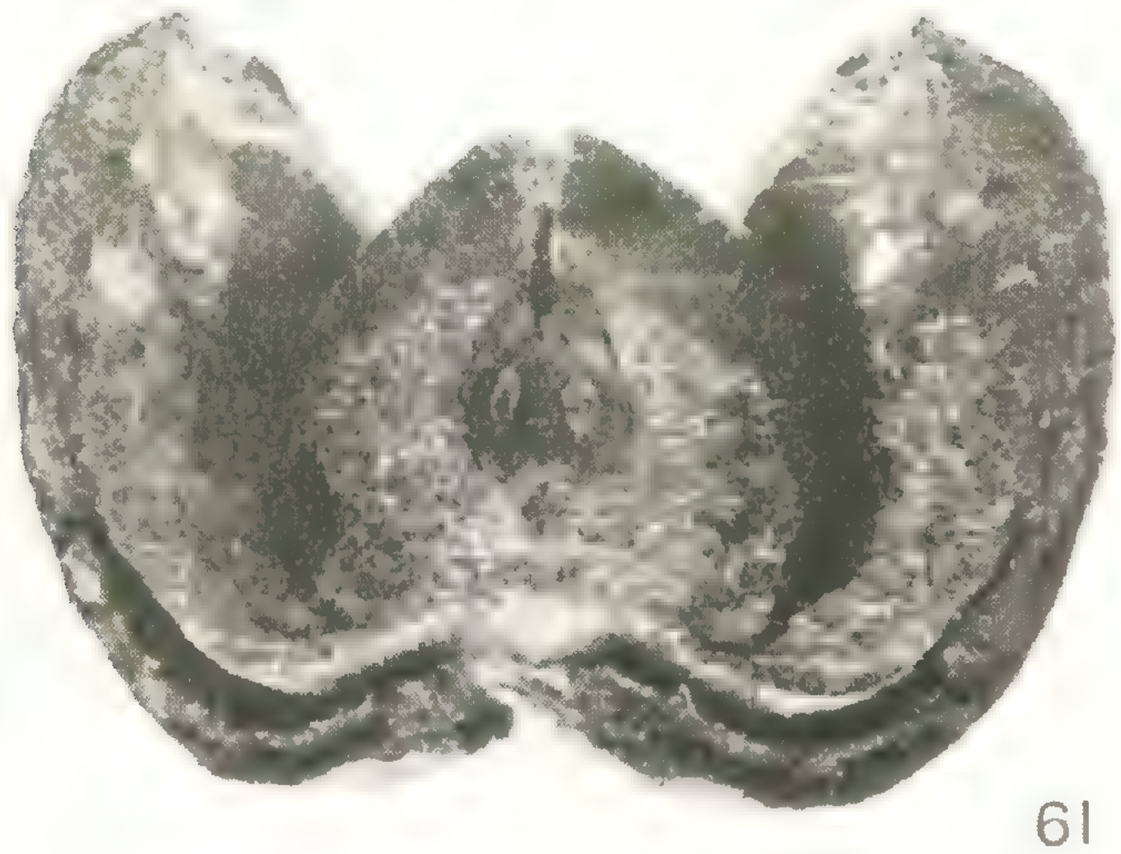

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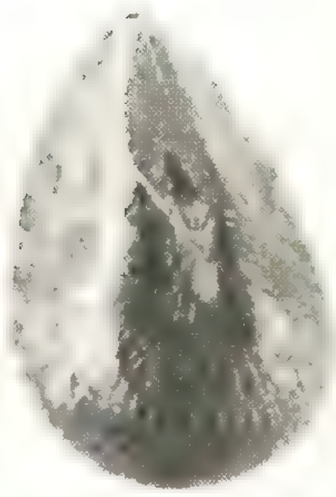

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WEBSTER, WEST INDIAN PHYLLANTHUS

NODAL ANATOMY IN RETROSPECT

I. W. Bailey

INTRODUCTION

In 1913, Professor E. W. Sinnott and I initiated a series of cooperative investigations on the phylogeny of the angiosperms which led us to the publication of nine papers betwen 1914 and 1918. Summations of evidence accumulated during the last forty years have supported and strengthened our contention (20) that ancestral angiosperms were relatively large woody perennials, and that the herbaceous habit in dicotyledons is a derived, rather than a primitive one. Similarly, much additional information has verified our conclusion (1) that the structure of the xylem in such representatives of the Amentiferae as the Casuarinacae, Betulaceae and Fagaceae is relatively highly specialized rather than truly primitive. On the contrary, our conclusions regarding the ancestral form and vasculature of the angiospermic leaf need reconsideration in the light of investigations of a wider range of material.

GENERALIZATIONS REGARDING NODAL ANATOMY

As a result of an extensive reconnaissance of 34 orders and 164 families of dicotyledons, Sinnott (18) emphasized the fact that there are three significant forms of foliar nodal anatomy in angiosperms, viz., the *unilacunar* form, in which the vascular supply of the leaf is related to a single gap in the stele, the *trilacunar* form, in which the vascular strands are related to three distinct and more or less widely separated gaps, and the *multilacunar* form, in which numerous lateral vascular strands are related to independent gaps. Although a number of dicotyledonous families are prevailingly unilacunar, trilacunar or multilacunar — thus providing significant evidence in the identification and classification of plants — there are a considerable number of families and numerous orders in which transitions between the different forms of nodal anatomy occur. Sinnott concluded that the trilacunar condition is primitive in angiosperms, the multilacunar form having arisen by amplification of the number of independently attached lateral strands, and the unilacunar form (a) in certain families, by the reduction and elimination of the two lateral strands and (b) in other families, by the approximation of the median and lateral strands forming an aggregation of three strands that is related to a single gap in the stele.

These conclusions, in which I concurred, were based upon putative phylogenetic evidence derived from the angiosperms as a whole, and upon ontogenetic sequences that occur in the developments of specific plants. The trilacunar condition tends to predominate in a majority of the families of the

Archichlamydeae, the unilacunar structure in the Centrospermae, Myrtiflorae and a majority of the families of the Metachlamydeae. The multilacunar condition is characteristic of many of the Polygonaceae, Platanaceae, Simarubaceae, Burseraceae, Meliaceae, Araliaceae and Umbelliferae. Transitions to unilacunar structures frequently occur in trilacunar families in representatives which exhibit an enhanced degree of both floral and anatomical specialization. Similarly, aberrant transitions to multilacunar nodal anatomy occur in many predominantly trilacunar orders and families. Where the leaves of adult plants are multilacunar, the first-formed leaves of seedlings commonly are trilacunar with transitions to the typical multilacunar condition in successively formed ones. Similarly, the first leaves of monocotyledonous seedlings frequently have three independently attached vascular strands, thus resembling the trilacunar-like structure that occurs in the adult leaves of putatively more primitive representatives of the Potamogetonaceae.

STATISTICAL CORRELATIONS REGARDING LEAF FORM

In a subsequent comprehensive survey of 156 families of dicotyledons, we (19) demonstrated that there is an evident correlation between nodal anatomy and the formation of stipules. Of 75 of these families, which have stipules or leaf sheaths, 53 are characterized by having trilacunar or multilacunar nodal structure, and in five others this form of nodal anatomy is common. In 16 of these stipulate families the nodes are unilacunar, but in 11 of them the stipules frequently are poorly developed, minute or absent. Conversely, of 81 exstipulate families 52 are characteristically unilacunar and two more are frequently so. Where unilacunar structure occurs in aberrant genera or species of dominantly stipulate and trilacunar families, such plants commonly exhibit reduction or elimination of stipules. Conversely, aberrant trilacunar representatives of dominantly unilacunar families not infrequently have well-developed stipules in contrast to their unilacunar relatives. Among exstipulate trilacunar families approximately 75% of the plants have leaves or leaflets with entire margins. Thus, the fullest development of stipules occurs in trilacunar families having lobed leaves or leaves with dentate, serrate or glandular margins, whereas the strongest tendency toward the reduction and elimination of stipules occurs in unilacunar families having leaves with entire margins. It is significant in these connections that the vasculature of most stipules is related to the lateral vascular strands at some level of the node or petiole.

As a result of extensive statistical analyses of dicotyledonous floras in diversified phytogeographical regions of the principal continental areas, we (21) concluded that the primitive angiospermic leaf was simple, palmately veined, probably 3-lobed, and was provided with three main vascular strands which were attached at a trilacunar node. These conclusions were based upon evidence from *paleobotany*, that the palmate leaf was more frequent in the Cretaceous and Tertiary than at present; from *comparative morphology*, (a) that there is a correlation between the palmate leaf and

trilacunar (and multilacunar) nodes, (b) that there is a strong correlation between the simple pinnate leaf and the unilacunar node, (c) that palmate or parallel venation tends to predominate in cotyledons and floral appendages; and from *phylogeny*, that palmate leaves are more frequent in relatively primitive groups of dicotyledons and that pinnate leaves are commoner in more advanced ones. Furthermore, among woody plants the trilacunar (more ancient) nodal condition predominates in temperate regions, and the unilacunar (more advanced) in the tropics. The palmately lobed leaf among woody plants is largely confined to temperate regions. These facts, in company with others, suggested that the dicotyledons first appeared under a climate more temperate than tropical, a climate in the Mesozoic presumably found extensively only in the uplands.

REVIEW OF PHYLOGENETIC EVIDENCE

The most comprehensive and reliable phylogenetic sequence thus far revealed among the higher plants is the derivation of vessels from scalariformly pitted tracheids in the angiosperms. As demonstrated by large volumes of data successively accumulated during the last 40 years, the complete evolutionary story is preserved among living angiosperms, and it is no longer essential to search geological strata for "missing links." Furthermore, this particular phylogenetic sequence clearly is a unidirectional and irreversible one, and cannot be read in reverse, as so frequently happens, since in view of available information regarding the structure of the lower vascular land plants tracheids cannot logically be derived from the dissociated members of vessels.

It should be emphasized in this connection that the evolution and specialization of vessels in angiosperms have been reconstructed *entirely independently* of assumptions regarding the relative 'primitiveness of specific orders, families or other taxa of the angiosperms. Although primitive vesselless forms of dicotyledonous xylem are confined at present to woody plants of putative ranalian affinities, viz., Winteraceae, *Trochodendron*, *Tetracentron*, *Amborella* and *Sarcandra*, relatively primitive stages in the evolution of vessels are preserved in such families of the Metachlamydeae as the Clethraceae, Ericaceae, Symplocaceae, Styracaceae and Caprifoliaceae, as well as in various families of the Archichlamydeae. Conversely, highly evolved and specialized vessels occur in many representatives of such putatively primitive taxa of the Archichlamydeae as the Amentiferae, Ranales, Rosales, Malvales, etc. Thus, it is now clearly demonstrated that evolutionary modification of the xylem of stems and roots is *not necessarily* closely synchronized with phylogenetic trends in the specialization of the angiospermic flower. Either trend of evolution may be accelerated or retarded in relation to the other. For example, among primitively vesselless genera of the dicotyledons, certain of them, e.g., *Zygogynum, Trochodendron, Sarcandra,* exhibit advanced stages of floral specialization. Therefore, although one of the various classifications of the angiosperms may possibly provide a fairly accurate picture of certain

aspects of floral evolution, it evidently does not afford a truly phylogenetic classification of the plants which bear the flowers, i.e., when evidence from all organs and parts of the plants is taken into consideration. Nor can a truly natural classification of plants as a whole be attained by substituting phylogenetic trends, however reliable, from another **single** organ or part of the plant.

In view of such facts as these, there obviously are inherent difficulties and dangers in attempting to determine the primitive form and vasculature of the angiospermic leaf by statistical analyses of the various families and orders of the Archichlamydeae as contrasted with the Metachlamydeae, or in basing conclusions upon speculative assumptions that have been made regarding the relative primitiveness of the Amentiferae, Ranales, Rosales, Malvales, etc.

In the case of the vessel, paleobotanical evidence demonstrates that it can be derived only by modification of *one* type of cell, viz., tracheid. On the contrary, in the case of the angiospermic leaf, the possibility exists that it may have been derived from one of *several* diversified forms of potentially ancestral foliar appendages. Furthermore, the possibility exists that changes in form and vasculature may at times be reversible. In other words, in the case of the vessel convincing evidence is now available regarding initial stages of a unidirectional and irreversible evolutionary trend, whereas in the case of the leaf no comparably reliable information is available as yet.

REVIEW OF NODAL ANATOMY

Sinnott's and my conclusions regarding the primitive form of the angiospermic leaf were based largely upon our contention that in angiosperms unilacunar and multilacunar nodal structures are derived from a primitive trilacunar one. Since a similar working hypothesis was subsequently adopted by Eames (6) in the study of floral appendages, it is evident that nodal anatomy became the keystone in a large volume of phylogenetic investigation. Thus, it is essential to determine how reliable a working hypothesis is provided by nodal anatomy.

Among ferns, seed ferns, Cordaitales, Bennettitales (*sensu lato*), Coniferales, *Ginkgo* and *Ephedra,* the vascular strands of the leaf, whether one, two or many, are related to a single gap in the primary body. Deviations from this prevailing *unilacunar* condition occur, however, in the living cycads and in *Gnetum*, where numerous foliar strands are related to an equivalent number of independent gaps in the stele. Such evidence from the lower Pteropsida suggests that a unilacunar type of node is primitive, and that the multilacunar condition among gymnosperms is a derived and specialized one. Therefore, the trilacunar and multilacunar structures of angiosperms must have been derived at some evolutionary stage from a unilacunar condition. Whether the transition occurred within the angiosperms themselves or during the evolution of their ancestors is a basic problem in need of solution. Are all forms of unilacunar nodes homologous or are there

fundamental structural differences that have been overlooked? If the early angiosperms acquired a pair of independently attached foliar strands and subsequently eliminated them by reduction or approximation. does the resulting unilacunar condition differ structurally from the primitive nodal anatomy of the lower Pteropsida?

Much of the work in the past has dealt with comparative investigations of fully matured structures at nodal levels. Such comparative studies of end products have proven to be of significant value in the identification and classification of plants, but, without comprehensive developmental investigations at successive levels of the shoot and leaf, they may be misleading at times in the study of phylogeny.

There has been an increasing tendency of late to visualize the vasculature of the stem and its appendages in terms of the "Telome Theory." Thus, particularly in the case of the Cordaitales and Coniferales, the leaf trace is illustrated as a single strand which may dichotomize one or more times in its upward extension into the leaf. In such plants there may be two separate vascular strands (related to a single gap) at the nodal level, with more or less numerous additional dichotomies occurring within the lamina of the leaf. It is significant in this connection, however, that in *Ginkgo biloba* L. as demonstrated by Gunckel and Wetmore (11, 12), in certain species of *Ephedra* (14, 15), and in such dicotyledons as *Austrobaileya* (3, 14), *Trimenia* (14, 16), *Ascarina* (22), *Lactoris* (23), and *Clerodendron trichotomum* Thunb. (14), although there are two separate vascular strands related to a single gap at the nodal level, these strands do not unite at lower levels but retain their individuality and are connected to *two entirely independent bundle systems of the eustele*. This raises the question whether there are two fundamentally different types of vasculature within the Pteropsida or merely extreme deviations from a single basic type.

In *Ginkgo*, the vasculature of the lamina is typically dichotomous, the veins of the two bilateral halves of the leaf being related, however, to two independent parts of the eustele. Therefore, the number of veins tends to be a multiple of two, viz., an *even* number. This is in marked contrast to the vasculature of many dicotyledonous leaves which tend to have an *odd* number of vascular strands at the nodal level. How does a transition from an *even* to an *odd* number of vascular strands occur?

In those representatives of the Coniferales which have a single vascular strand in the leaf and at nodal levels, the vasculature might be due to a suppression of dichotomies correlated with extreme reduction in the breadth of the lamina of the leaf. On the contrary, in dicotyledons which have relatively broad leaves and a single vascular strand at the nodal level, the strand frequently is resolved at subnodal levels into two independent traces. In other words, the single strand at the nodal level may be interpreted as having evolved by *fusion* of *two* independent traces rather than by suppression of the dichotomy of a *single* trace.

In this connection, recent investigations of the Chloranthaceae, Lactoridaceae, Amborellaceae, Trimeniaceae, Austrobaileyaceae, Monimiaceae,

Lauraceae, Gomortegaceae and Hernandiaceae have revealed considerable significant evidence. The *totality* of morphological characters from different organs and parts indicates that these families are relatively closely related and constitute one of two major categories of the woody Ranales (*sensu lato*). With a few exceptions, which will be discussed subsequently, all of the numerous genera have prevailingly unilacunar nodes and simple leaves with characteristically pinnate venation. The xylem of the various genera exhibits numerous successive evolutionary stages in the development of vessels; that of *Sarcandra* (24) and *Amborella* (2) being of a primitive vesselless form, whereas that of the Hernandiaceae contains vessels of a highly evolved and specialized structure.

In *Ascarina* (22), *Austrobaileya* (3), *Lactoris* (23) and *Trimenia* (16), there are two independent foliar traces which extend upward to the nodal level and into the petiole of the leaf. These vascular strands may remain distinct and separate throughout the costa of the lamina or they may fuse to form a single mid-vein, particularly in the middle and upper parts of the lamina. Thus, each bilateral half of the simple, pinnately veined leaf is vascularized by minor lateral ramifications of an independent foliar trace. In *Amborella* (2) and in certain representatives of the Monimiaceae (16) fusion of the two principal strands to form a single broad arc of vascular tissue extends downward to the nodal level, giving the impression, *except at lower levels*, that the leaf is vascularized by a single foliar trace.

In *Piptocalyx* (16), a close relative of *Trimenia*, the two independent traces tend to dichotomize, forming four strands in their upward course toward the base of the leaf. The two central strands commonly fuse at the nodal level or in the basal part of the petiole, thus exhibiting a transition from an *even* number (four) to an *odd* number (three) of foliar vascular strands. Numerous representatives of the Monimiaceae likewise have an odd number (three, five, seven, nine) of strands at the nodal level. That these strands commonly result from the bifurcation of two independent traces may be demonstrated by tracing them downward through two internodes of the stem. In many cases at least, the odd number of strands at the nodal level is due to the fusion of strands that belong to two independent systems of vasculature. Such a pattern of dichotomy and fusion occurs in many species of *Hedyosmum* (22), where there are usually five strands at the nodal level and in the base of the petiole.

In all of the numerous genera of these families, with the possible exception of *Sarcandra* and *Chloranthus*, there is no evidence which may be interpreted as indicative of the derivation of a unilacunar from a trilacunar form of nodal structure. The occurrence of three strands (as well as one, two, four, five, six, seven or nine) at the nodal level cannot be accepted as unquestionable evidence of a transition to unilacunar vasculature by the approximation of three separate strands of a trilacunar node.

Within the Chloranthaceae (22) *Ascarina*, as previously noted, has two independent traces which pass upward to the nodal level and extend out-

ward through the petiole into the lamina of the leaf. In *Hedyosmum* the two traces divide in their upward course, forming six strands, the two slender central members of which tend to unite at the nodal level. Thus, at this level, the leaf appears to be vascularized by an odd number (five) of primary strands. *Sarcandra* and *Chloranthus* resemble *Ascarina* in having two massive independent traces which extend upward into the leaf. Most of the bilateral vasculature of the pinnately veined lamina is related to these two conspicuous strands. However, the basic pattern of vasculature is complicated in the petiole and at the nodal level by the occurrence of three small additional strands. The medianly located one of these is formed, as in *Hedyosmum*, by the fusion of minor branches of the two subtending leaf traces. The other minor strands are laterally situated and are related to independent traces at separate gaps in the eustele. In most dicotyledons having opposite leaves and trilacunar structure, there are six gaps at the nodal level, i.e., three independent gaps for each leaf, compare *Fig. 1, G*. In *Sarcandra* and *Chloranthus* there are four gaps, two median ones facing the leaves as in *Ascarina* and *Hedyosmum* and two lateral ones in addition. The corresponding lateral strands of the two leaves fuse at the nodal level and are jointly related to these gaps, compare *Fig. 1, F*. However, at lower levels they separate and become attached to independent parts of the eustele. *A priori* there is no convincing evidence for interpreting this aberrant form of vasculature as a transition from trilacunar to unilacunar nodal structure rather than *vice versa*. Indeed, the totality of evidence indicates that there is a fundamental *double* system of vasculature throughout all representatives of this group of families; transitions from an even to an odd number of vascular strands occurring at different levels. Furthermore, it suggests that pairs of independently attached lateral strands may be added without necessarily modifying the number of principal strands that are related to the median gap in the eustele.

There are other categories of dicotyledons where a summation of evidence is indicative of a transition from unilacunar to trilacunar or multilacunar nodal anatomy rather than *vice versa*. For example, a majority of the Ericales are characterized by having simple pinnately veined leaves and unilacunar nodes. However, there is an aberrant tendency in the Epacridaceae, as in the Thibaudieae of the Ericaceae, to form leaves with palmately parallel venation. As emphasized by Dormer (5), only five of the more than twenty genera of the Epacridaceae have leaves with sheathing bases. Two of these, *Richea* and *Dracophyllum*, differ markedly from the rest of the Epacridaceae, and from other representatives of the Ericales, in having trilacunar and multilacunar nodes. Thus, in the case of the Epacridaceae, as of the Chloranthaceae, a *totality* of evidence is indicative of the derivation of trilacunar and multilacunar nodes from a unilacunar one. This is in marked contrast to conditions in such families as the Leguminosae, Anacardiaceae, etc., where certain genera or species exhibit reduction from trilacunar to unilacunar nodes.

A summation of evidence from the dicotyledons as a whole indicates,

therefore, that conspicuous modifications of nodal structure are reversible, pairs of independently attached lateral strands being added in certain cases and eliminated in others. Furthermore, the addition or subtraction of pairs of independently attached strands can occur without fundamental changes in the number of the vascular strands related to the median gap of the node. Thus, more emphasis should be placed in the future upon studying vascular tissues related to the median gap and upon tracing their extensions downward into lower levels of the stem. Transitions from an *even* to an *odd* number of traces appear to be of considerable significance in the phylogeny of the Pteropsida and in discussions of "Telomic" interpretations of vascularization patterns.

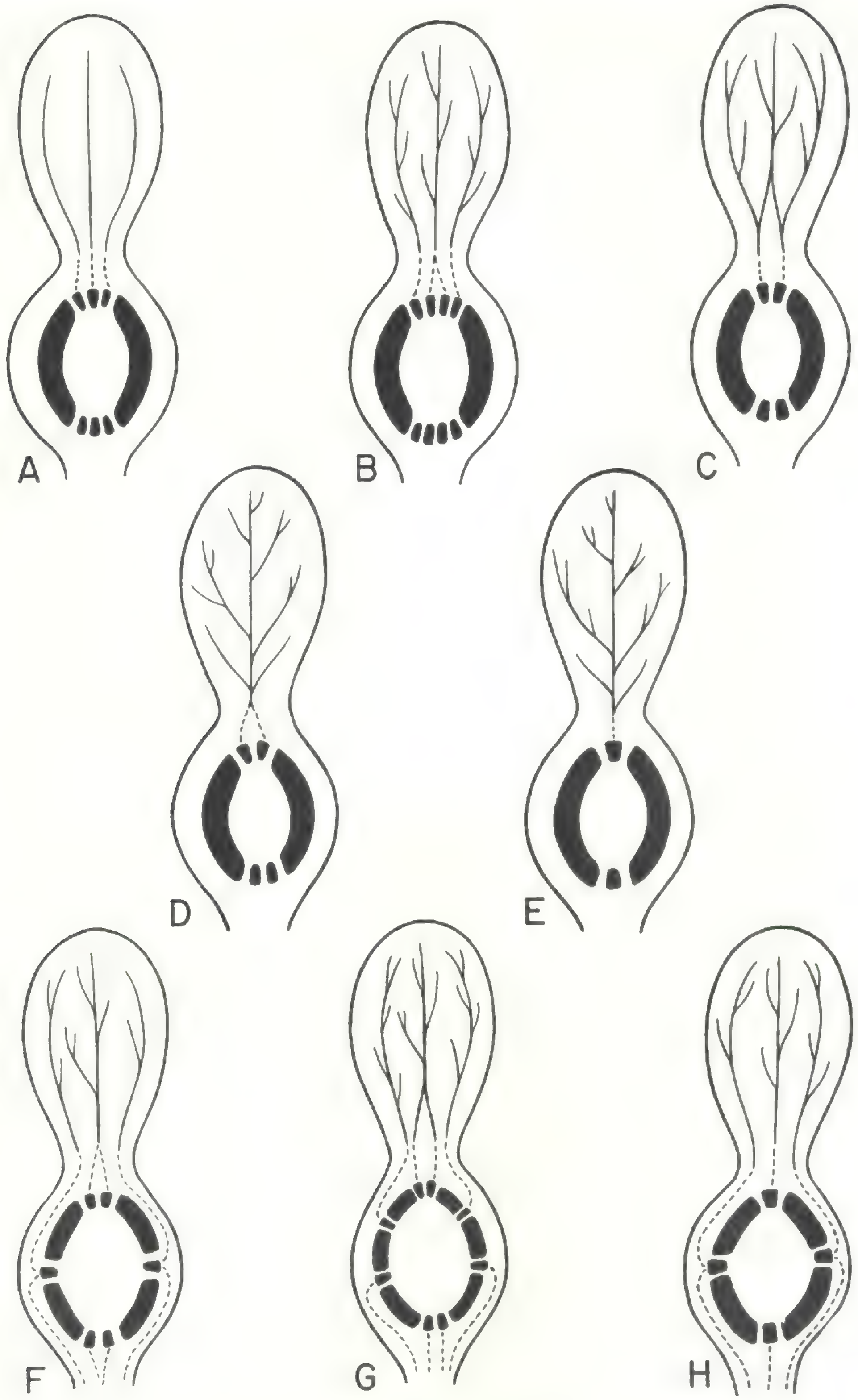
DEVELOPMENTAL INVESTIGATIONS

At present there is a dearth of reliable information regarding the extensions of leaf traces below the nodal level. Successive stages in the development of procambium, phloem, and xylem have been investigated by adequate modern techniques in a very limited number of genera and species. However, Nägeli's (17) numerous illustrations, coupled with the detailed investigation of *Linum* by Esau (7, 8) and Girolami (10), of *Sambucus* and *Helianthus* by Esau (9), and my own preliminary studies of a considerable number of dicotyledons, indicate that the leaf trace related to the median gap of the node (when followed downward) frequently forks above the next subtending leaf of an orthostichy. In other words, the halves of the leaf trace are related at lower levels to two independent parts of the eustele. This suggests (from ontogenetic and phylogenetic points of view) a fusion of two independent strands, and does not support telomic illustrations of a single trace which dichotomizes in its upward extension. Furthermore, the lateral traces of trilacunar and multilacunar nodes do not unite in most cases to form a single strand at lower levels.

NODAL ANATOMY AND VASCULATURE OF SEEDLINGS

As demonstrated in Lubbock's (13) comprehensive treatment of dicotyledonous seedlings, a majority of their cotyledons are simple and entire. However, there is a wide range of variability in form from broadly elliptical, orbicular, ovate, obovate, cordate or reniform to oblanceolate, spatulate or linear, and from sessile to extensively petiolate. Although palmately lobed, trifid, tripartite or multifid cotyledons are comparatively rare, emarginate, bilobed, bifid and auriculate forms are of not infrequent occurrence in various families.

As emphasized by Lubbock and others, there is a striking difference in form between the cotyledons and leaves of specific seedlings. This is particularly conspicuous in families having serrate, dentate, lobed, cleft, divided or compound leaves. Instances, e.g., Onagraceae, where the cotyledons assume a form during the later stages of their enlargement which



TEXT-FIG. 1. A–H, forms of cotyledonary nodal anatomy in dicotyledons.

closely resembles that of the first-formed leaves, are of exceptional rather than of common occurrence. In other words, although there is a similar range of variability in the form of cotyledons as among leaves, similar forms of cotyledons and leaves rarely occur in close association on the same seedling.

A reconnaissance of seedlings obtained from 99 families of the dicotyledons reveals a range of variability in cotyledonary nodal anatomy that is illustrated in *Fig. 1*. These patterns resemble structures that are known to occur at foliar nodes having opposite leaves. It is significant in this connection, however, that cotyledons with multilacunar attachments are rare, and that the frequency of occurrence of the unilacunar and trilacunar forms differs considerably in the case of cotyledons as contrasted with leaves.

Among cotyledons of the species investigated, 77% have an *even* number of vascular strands at the nodal level (*B*, *C*, *D*, *F* & *G*), and 60% of them have *two* independent traces that are related to a single gap (*C* & *D*). The latter double-trace, unilacunar form of nodal structure is not confined to a few specific genera, but evidently is of common occurrence in many orders and families of the dicotyledons. This is in marked contrast to foliar nodes where a large majority of dicotyledonous leaves are reported to have an *odd* number of traces and where the double-trace unilacunar form of structure has been encountered thus far in a limited number of families, viz., certain representatives of the Austrobaileyaceae, Trimeniaceae, Chloranthaceae, Lactoridaceae, Verbenaceae, Labiatae and Solanaceae.

Of the cotyledonary nodal patterns illustrated in *Fig. 1*, (*B*), present in 7% of the seedlings investigated, and forms (*F*) and (*G*), in 10% of them, are apparently of infrequent occurrence at foliar nodes. Form (*B*) has, however, been encountered at certain of the foliar nodes of *Piptocalyx* and form (*F*) at those of *Sargentodoxa*. On the contrary, form (*A*), having *three* strands related to a single gap, is of less frequent occurrence at cotyledonary nodes although commonly encountered at foliar ones.

In the case of leaves arranged in an opposite or decussate phyllotaxy and having one pair of independently attached lateral vascular strands, there usually are, as previously stated, six gaps at the nodal level, viz., three related to each of two leaves. Although this type of structure occurs at times at cotyledonary nodes (*G*), it is much less common than the arrangement illustrated in patterns (*F*) and (*H*) where the corresponding laterals of the two cotyledons unite and are related to two, instead of to four, independent lateral gaps. Although uncommon, this modification of trilacunar structure occurs as previously stated at the foliar nodes of *Chloranthus* and *Sarcandra*, and has been encountered at those of certain representatives of other families, e.g., Rubiaceae.

Thus, a reconnaissance of seedlings indicates that there is a range of structural variability in cotyledonary nodes similar to that found in foliar ones. The fundamental differences between the vasculature of leaves and cotyledons at the nodal level are quantitative rather than qualitative, an

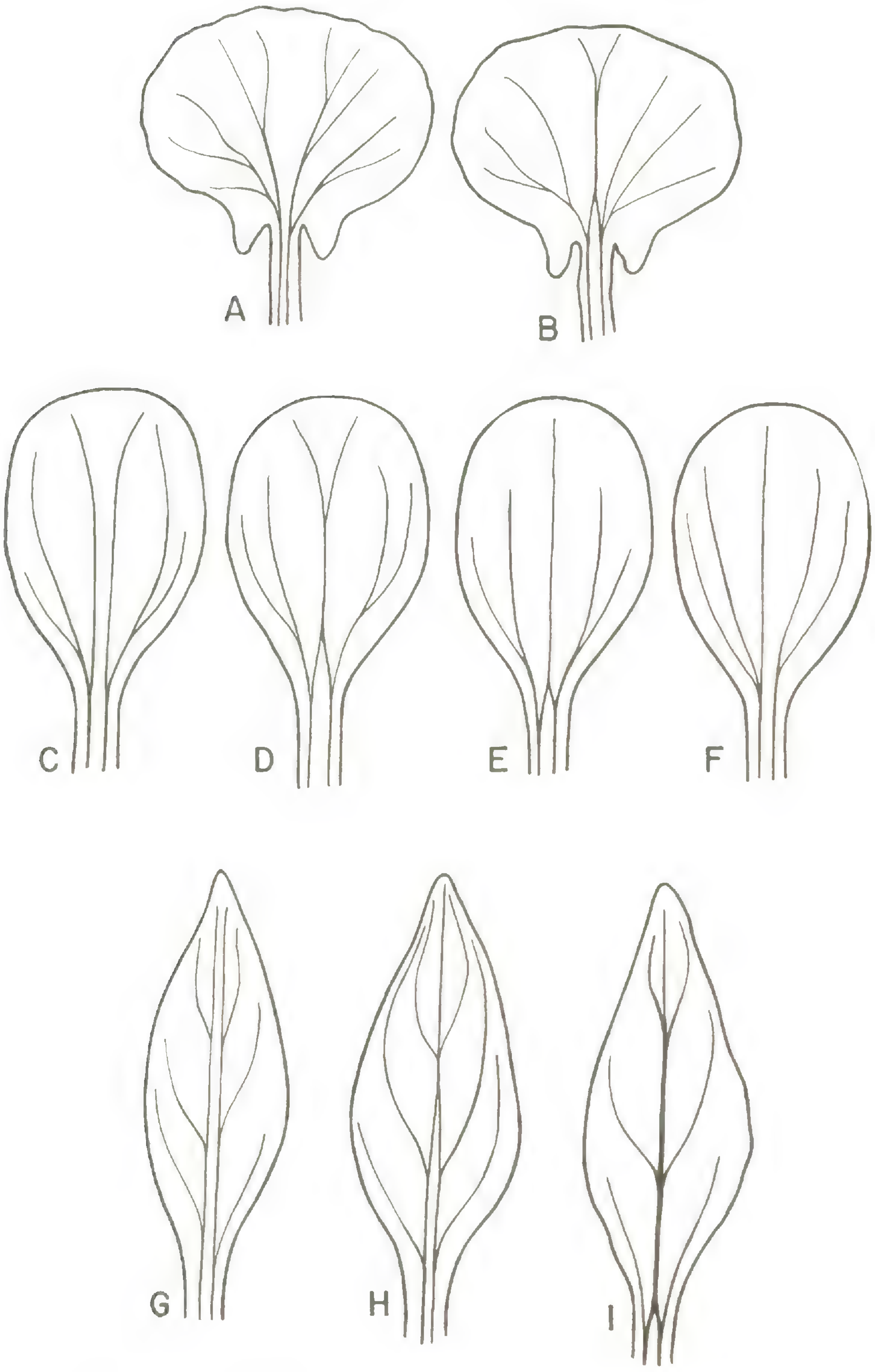
even number of vascular strands being commoner in the case of cotyledons and an *odd* number in the case of leaves

It should be noted in this connection, however, that cotyledons with multilacunar attachments do not occur in any of the seedlings that I have studied, even in families where the leaves of adult plants are attached at multilacunar nodes. Although cotyledons with pentalacunar vasculatures have been demonstrated by Carlquist (4) to occur in *Fitchia speciosa* Cheeseman, there are reasons for believing that multilacunar attachments will prove to be of infrequent occurrence in the dicotyledons as a whole. In families having multilacunar foliar nodes, e.g., Magnoliaceae, Polygonaceae, Umbelliferae, etc., the leaves are arranged prevailingly in alternate rather than in opposite phyllotaxy. There appear to be spatial and other difficulties in the development of multilacunar nodes where the leaves are opposite. Furthermore, as previously noted, where the leaves of adult plants are multilacunar the first leaf of the seedling commonly tends to be trilacunar with transitions to the typical adult multilacunar condition occurring in subsequently formed leaves of the young plant. The cotyledonary nodes of such plants are either of the unilacunar type (viz., having two gaps, one for each of the opposite cotyledons) or of the trilacunar forms illustrated in (*F*), (*G*) and (*H*). In this respect, the seedlings of such plants with multilacunar foliar nodes resemble those of the multilacunar living cycads and *Gnetum*.

It should be emphasized in this connection that, if the trilacunar condition is primitive in angiosperms, and if the ontogenetic sequences in the preceding paragraph are to be interpreted as recapitulations of the phylogenetic derivation of multilacunar nodes from trilacunar ones, then one might anticipate finding ontogenetic sequences in seedlings illustrating the reduction of trilacunar nodes to unilacunar ones. Although a considerable number of seedlings that I have examined have a first-formed leaf attached at a unilacunar node in contrast to the trilacunar or even the multilacunar nodes of the adult plant, I have not succeeded thus far in finding a succession of seedling leaves which exhibit an ontogenetic transition from trilacunar to unilacunar structure.

As previously emphasized by Sinnott and myself (21), many cotyledons are characterized by having a pseudo-palmate or palmate-parallel venation. In such cotyledons, there commonly are three or five conspicuous primary veins that extend outward from a locus at the base of the cotyledon, the lateral ones diverging and extending parallel to the margins of the lamina, *Fig. 1, C, Fig. 2, E.* A large number of these cotyledons show a transition from an *even* number (two) of vascular strands at the nodal level to an *odd* number (three or five) of primary veins in the lamina. The outward extensions of the two independent traces commonly divide in the petiole or the base of the lamina, forming four or six strands, the two central members of which unite to form a mid-vein, *Fig. 2, E.*

There are numerous deviations and aberrations of this common form of pseudo-palmate vasculature, not only among different families and genera, but also among seedlings of the same genus or species. The branches of



TEXT-FIG. 2. A–I, forms of cotyledonary venation in dicotyledons.

the two traces may remain independent throughout the lamina, *Fig. 2, A* & *C*, or the two central ones may approximate and then diverge toward the apex of the cotyledon, *Fig. 2, D*. Where the branching is symmetrical, *Fig. 2, A* & *C*, there is an *even* number of conspicuous veins in the lamina. On the contrary, where the branching is asymmetrical, as sometimes happens, *Fig. 2, F*, a single branch of one trace may assume the position of a mid-vein, and there may be an *odd* number of conspicuous veins in the lamina.

The phenomena of dichotomy and fusion, which lead to a transition from an even to an odd number of vascular strands, may occur at different levels of the lamina, the petiole or the nodal and subnodal regions. Where the dichotomy is precocious, there may be four or even six strands related to a single gap at the nodal level, *Fig. 1, B*. Conversely, where the concrescence of independent strands is precocious, there may be a single strand at the node, *Fig. 1, E*, or in the petiole, *Fig. 1, D*, with one, three or five conspicuous veins diverging from it in the base of the lamina. Where both dichotomy and concrescence are precocious, there may be three strands related to a single gap at the nodal level, *Fig. 1, A*. In the case of cotyledons having more than two strands at the level of attachment, two or more of the basal lateral veins of the lamina commonly are in direct continuity with independent traces, related either to a single gap, *Fig. 1, A* & *B*, or to independent lateral gaps, *F, G*, & *H*.

It should be noted in this connection that there are numerous cotyledons which exhibit intermediate or transitional forms of vasculature between these pseudo-palmate patterns and typically pinnate ones In such cotyledons, the basal lateral veins are less conspicuous and extensive and the apical branches of the mid-vein are correspondingly emphasized, *Fig. 2, H* & *I*. It is significant, however, that even the narrower forms of pinnately veined cotyledons commonly exhibit a vasculature that is related at some level to two independent vascular strands or traces. As in the pinnately veined leaves of *Austrobaileya*, *Trimenia* and *Ascarina*, two traces may extend independently throughout a cotyledon, *Fig. 2, G*, or they may become concrescent at varying levels of the lamina, *Fig. 2, H*, of the petiole, *Fig. 2, I*, or of the node, *Fig. 1, E*.

There appears to be no conspicuous and universal correlation between the form and venation of cotyledons and specific types of nodal structure. Cotyledons of widely varying form and venation may have a similar basal vasculature. Conversely, cotyledons of similar form may be attached at strikingly different nodes. However, there does appear to be a higher percentage of pinnate venation among cotyledons which are attached at single-trace unilacunar nodes.

Occasionally there is a considerable range of variability in the vasculature of cotyledons grown from the seed of a single plant, and at times in the two cotyledons of a single seedling. For example, one cotyledon may have four vascular strands related to a single gap at the nodal level, *Fig. 1, B*, whereas the opposite cotyledon has one or two of these strands attached at independent gaps, *Fig. 1, G*. The branches of two traces

may extend independently throughout the lamina of one cotyledon, *Fig. 2, A, C, F & G*, whereas approximation and concrescence of branches to form a mid-vein occur in another cotyledon, *Fig. 2, B, E, H & I*.

VASCULATURE OF FLORAL APPENDAGES

The nodal anatomy of floral bracts, bracteoles, and the independent parts of polysepalous calyces frequently resembles that of the leaves of the plant upon which the flowers are borne. However, there are numerous deviations, and the venation of free sepals, as of petals, tends in many cases to be pseudo-palmate even where the leaves have a typical pinnate venation. The folded megasporophylls of apocarpous flowers also tend to have a palmate-parallel venation, the basal vasculature varying from unilacunar to trilacunar to multilacunar. According to Eames (6), the 3-veined (one dorsal and two ventrals) trilacunar form of carpel is primitive, the unilacunar and multilacunar forms having developed from it by obvious trends of simplification and amplification. Most stamens have a single vascular strand that is related to a unilacunar node.

Recent investigations of a number of the less well known tropical and subtropical representatives of the woody Ranales (*sensu lato*) have revealed evidences of what appear to be primitive forms of floral morphology. Among such plants there are various stages in the differentiation of sterile appendages into bracteoles, sepals and petals. There are broad microsporophylls which are not differentiated into filament, anther and connective, and unsealed, styleless megasporophylls with widely diffused stigmatic surfaces.

The carpels of the less specialized flowers of the Winteraceae resemble conduplicately folded, emarginate, pseudo-palmate, 3-veined cotyledons. The microsporophylls and staminodes of *Degeneria* and *Himantandra* also have a palmate-parallel, 3-veined vasculature, as do many of the stamens of the Magnoliaceae. Such occurrences strengthen Eames's contention that primitive carpels and stamens were conspicuously 3-veined sporophylls. In the case of carpels, the elimination of a stipe, incipient adnation to the torus, sterilization of the upper part of the megasporophyll as a concomitant of the formation of a style, reduction in the number of ovules, and diverse forms of adnation and cohesion tend more or less extensively to modify this primitive vasculature. In the case of the stamen, reduction in the lamina of the microsporophyll, increasing protuberance of the sporangia, and the formation of a comparatively slender filament appear to have resulted in the suppression and elimination of the lateral veins, leaving a single median vascular strand.

Although the venation of relatively primitive forms of carpels and stamens tends to be comparatively stable within a flower, their vasculature at nodal and subnodal levels commonly is variable even in a single specimen, as might be anticipated from a developmental point of view where numerous appendages are congested upon the broadened apex of a pedicel. The three principal veins of one carpel or stamen may be

related to a single trace (unilacunar) at the nodal level, those of another may be related to three approximated traces (unilacunar), whereas those of a third are related to three widely separated traces (trilacunar).

Transitions from an even (two or four) to an odd (one or three) number of vascular strands are apparently of infrequent occurrence even in the subnodal levels of floral axes. However, in *Austrobaileya* (3) the dorsal vein of the carpels, the mid-vein of the broad microsporophylls, and the veins of the staminodia, tepals and bracteoles are related at lower levels to two separate traces which are related in turn to two separate parts of the eustele. Furthermore, in the case of *Sarcandra* (24), a vesselless representative of the Chloranthaceae, there is a single stamen that is basally adnate to a carpel. The mid-vein of the stamen usually is double. Not only may the paired veins run independently throughout the stamen, but also they are related at lower levels to two independent bundles of the eustele. Transitions from *two* independent strands to *one* occur at times and at different levels by concrescence of the two strands. The carpel of *S. glaber* has a double dorsal vein and two ventrals which may be widely separated or closely approximated. The carpel of *S. hainanensis*, on the contrary, not only has a single dorsal vein, but also a single ventral one due presumably to the concrescence of two ventral veins or to the suppression of one of them.

Although detailed developmental investigations are likely to reveal additional instances of doubleness in the subtending traces of floral appendages, it is unlikely that transitions from an even number of traces to an odd number of principal veins will prove to be of as frequent occurrence in the case of stamens and carpels as in the case of leaves and particularly of cotyledons.

It should be noted in these connections that cotyledons and floral appendages are of comparatively limited size, and rarely, if ever, have stipules or a truly compound lamina. Furthermore, where they have the homologue of a petiole, the vasculature does not attain the extreme complexities that occur in the petiole and costa of many leaves. With the exclusion of compound leaves and excessive petiolar complexities, one finds a similar range of potentialities of form and vasculature in cotyledons and floral appendages as in simple leaves with pinnate or palmate venation. The differences between various categories of appendages are quantitative rather than qualitative. Two-trace unilacunar nodes and transitions from an even to an odd number of vascular strands are apparently of decreasing frequency in passing from cotyledons to leaves to stamens and carpels.

DISCUSSION

The data recorded on preceding pages indicate that it is no longer possible to assume that unilacunar nodes in dicotyledons are derived *in all cases* by reduction from a trilacunar condition. Although reduction of trilacunar nodes to unilacunar ones in dicotyledons may ultimately prove

to be of more common occurrence than the reverse phenomenon of amplification from unilacunar to trilacunar, this can be determined with certainty only by more comprehensive and laborious investigations of individual families and orders.

A summation of extensive evidence from the Ranales (*sensu lato*) suggests that during early stages of the evolution and diversification of the dicotyledons, or of their ancestors, certain of the plants developed trilacunar nodes, whereas others retained the primitive unilacunar structure that occurs so characteristically in ferns, seed ferns, Bennettitales (*sensu lato*), Cordaitales, Coniferales, *Ginkgo* and *Ephedra*. Furthermore, a broad survey of seedlings of both dicotyledons and monocotyledons — as well as of those of the living cycads and *Gnetum* — indicates that, where adult plants have developed trilacunar and multilacunar nodes, the cotyledons and first juvenile leaves commonly exhibit a retardation or inhibition of the tendency to form one or more pairs of independently attached lateral traces.

In addition, a summation of seedling evidence accentuates the significance of the occurrence of two independent systems of foliar vasculature in such dicotyledonous families as the Austrobaileyaceae, Trimeniaceae, Chloranthaceae and Lactoridaceae It necessitates a re-evaluation of the "Theory of the double leaf trace" briefly outlined in 1907 by Thomas (25).

It should be emphasized in this connection that the double-trace unilacunar form of vasculature of leaves, *as of buds*, is significant from physiological, as well as from morphological points of view. An actively transpiring appendage with this form of attachment is able to tap more conducting tissue of the primary body of the main axis than it would be able to do if connected to a single vascular strand at lower levels of the eustele. Transitions from unilacunar to trilacunar and multilacunar structures not only insure more numerous contacts with the conducting strands of the eustele of the stem, but also can provide mechanically stronger attachments at the nodal level.

It is of interest, accordingly, to inquire whether a double-trace pattern of vasculature is a primitive basic form in Pteropsida from which others have been derived by various trends of structural modification. Does a single-trace unilacunar structure arise in all cases by the approximation and fusion of two originally independent vascular strands? Data obtained from nodes and leaves of adult shoots, without reliable information regarding the development and attachment of leaf traces in subnodal parts of the stem, are inadequate for fully answering the question. Although the vascular tissues related to unilacunar nodes, and to the median gap of trilacunar ones, have been demonstrated in an increasing number of cases to be related at lower levels of an orthostichy to two independent parts of the eustele, it is not known at present whether such attachments predominate in the dicotyledons and in various categories of the gymnosperms. Nor is there reliable evidence to indicate how extreme reductions in the size of leaves, and various xerophytic adaptations, may modify patterns of vasculature. However, reductions of trilacunar to unilacunar nodes

appear in certain dicotyledonous families to be correlated with such modifying factors. Accurate developmental investigations of the Coniferales may prove to be particularly significant in studying the effects of xerophytic tendencies.

It should be noted in passing that the vascular tissues of the primary body are described in terms of steles, bundles, traces and veins. However, in growing shoots of dicotyledons, the leaf traces are composed of long files of vertically contiguous tracheary cells. The individual files may be in contact laterally or they may be separated by parenchymatous elements. During the earlier stages of growth (after the acropetal development of the procambium) they differentiate successively from loci in the base of the leaf, and eventually extend from the lamina of the leaf downward through a varying number of internodes of the stem. From the point of view of translocation, they provide convenient precursors in the development of vessels. Furthermore, even when aggregated in a single trace, they provide independent channels of rapid movement into each bilateral half of a leaf. Thus, traces and veins may be regarded as aggregations of independent channels of rapid translocation, rather than as the most significant units in a system of conduction.

As previously stated, Sinnott and I (21) concluded that the primitive angiospermic leaf was simple, palmately veined, probably 3-lobed, and was provided with three main veins which were attached at a trilacunar node. The occurrence in certain dicotyledonous families of transitions from unilacunar to trilacunar structures and from pinnate to palmate-parallel venation indicates that the evolution of leaf form and vasculature is not a strictly unidirectional and irreversible phenomenon as in the case of the phylogeny of the angiospermic vessel. Furthermore, although relatively primitive forms of carpels and stamens have three conspicuous primary veins, evidence from cotyledons and from the leaves of a number of ranalian and other families raises the possibility that the mid-vein of angiospermic appendages may have evolved by the approximation and fusion of branches of two independent systems of vasculature. However, it should be freely admitted in conclusion that critical paleobotanical evidence is not available as yet for solving the problem of the ancestry of the angiosperms or of the primitive form and vasculature of their appendages.

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HARVARD UNIVERSITY HERBARIUM
CAMBRIDGE, MASS.

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STUDIES IN THE BORAGINACEAE, XXVIII. NEW OR OTHERWISE INTERESTING SPECIES FROM AMERICA AND ASIA

IVAN M. JOHNSTON

Cordia (§ Varronia) **lauta**, sp. nov.

Frutex 1.5–2 m. altus; ramulis 5–7 mm. crassis antrorse fulvo-strigosis (pilis ca. 1 mm. longis); foliis ellipticis evidenter venosis 8–12 cm. longis 5–7 cm. latis medium versus vel paulo infra medium latissimis utroque angulatis, margine evidenter irregulariterque serratis, supra fulvescentibus abundanter strigosis (pilis rectis 0.5–1 mm. longis e basibus disciformibus ca. 0.2 mm. diametro erumpentibus), subtus pallidioribus juventate plus minusve tomentulosis (pilis curvatis vel subtortuosis albis vel griseis gracilibus plerumque ca. 0.5 mm. longis); petiolis crassis 5–10 mm. longis fulvo-strigosis; pedunculo perelongate 10–30 cm. longo 3–4 mm. crasso terminali vel internodali; inflorescentia capitata ante anthesin 3–3.5 mm. diametro; calyce in alabastro obovoideo 12–16 mm. longo apicem versus 7–8 mm. crasso supra medium strigoso sessili, lobis triangularibus 4–4.5 mm. longis basi 3–4.5 mm. latis acutis fere ad apicem appendiculis liberis crassiusculis ad 1.5 mm. longis donatis; corolla conspicua alba infundibuliformi 6.0–7.8 cm. longa glaberrima 6–7-mera, limbo 4–5 cm. diametro; lobis ad 20 mm. latis ad 5 mm. longis rotundis vel subtruncatis, tubo ad 3 cm. longo nervis validis 12 vel 14 donato basi imo ca. 5 mm. crasso 1.5–2 cm. supra basim ca. 3 mm. crasso deinde sursum ampliato; staminibus 6–7 inclusis; antheris 4 mm. longis ad 1 mm. latis paulo infra medium affixis basi 1.5–7 mm. profunde lobatis apice emarginatis, supra medium connectivo lato encrassato donatis; filamentis 30–35 mm. longis filiformibus 3–3.5 mm. supra basim corollae affixis, ca. 1–5 mm. infra basim sinuum limbi corollae attingentibus; pollinis sphaericis ca. 160 μ prominenter abundanterque papillatis et minute punctulatis oribus circularibus 3 donatis; stylo 75–80 mm. longo e corolla breviter exserto, apice ca. 2.5 mm. profunde lobatis, lobis ca. 1 mm. profunde lobulatis; stigmatibus 4 capitatis terminatis; fructu ignoto.

MEXICO: Plan de Barrancas, Jalisco, steep rocky volcanic slopes, 2500–3500 ft. alt., shrub 1.5–2 m. tall, with white flowers, July 17, 1951, *H. S. Gentry & C. L. Gilly 10878* (TYPE, Arn. Arb.).

A species notable for its robust habit, coarse, very elongate peduncles, large calyces, and very large corollas. The corollas are certainly the largest known in the section Varronia and, furthermore, are larger than those of any other American member of the genus *Cordia*. The pollen is notable for its large size and its verrucose surface. Relationships of the species are uncertain. It must be classified with those Varronias having distinctly

capitate, terminal or extra-axillary inflorescences and simple, non-stellate indument. It has, however, no evident relationship with any of the members of that assemblage either north or south of the Equator. The species is one of the most distinct members of its genus that has been discovered in America during the past quarter century.

Cordia salvifolia Juss. ex Poir. Encyc. 7: 46 (1806).

Cordia Buchii Urban, Symb. Ant. 1: 475 (1900).

The type of *Cordia salvifolia* is in folder no. 6476 of the Jussieu Herbarium at Paris. A recent examination of the specimen reveals it to be a sterile branch of the endemic species of the island of Hispaniola which Urban described under the name *Cordia Buchii*. It does not represent the shrub of the Lesser Antilles which has been accepted as "*Cordia salvifolia*" for over a century. The label associated with Jussieu's type bears only the following data: "*Cordia salvifolia* J., donne par M. Dupuis".

Cordia (§ Varronia) **nesophila,** sp. nov.

Frutex 1–3 m. altus; ramis hornotinis 2–4 mm. crassis strigosis (pilis rigidis 0.1–0.4 mm. longis); foliis lanceolatis vel elliptico-lanceolatis 5–12 cm. longis 2–5 cm. latis, apice acutis, basi acutis vel plus minusve rotundis in petiolum 8–12 mm. longum abrupte contractis, margine dentatis vel dentato-crenatis, in facie superiore scabridis (setis minutis rigidis ascendentibus vel appressis e basi incrassata vel discoidea erumpentibus 0.1–0.5 mm. longis), in facie inferiore pallidioribus (pilis tenuioribus mollibus brevibus curvatis secus nervos gestis); nervis foliorum supra impressis, subtus prominentibus, primariis utroque latere costae 8–14 sub angulo ca. 45° abeuntibus vix vel parvum arcuatis, secundariis et tertiaris areolato-anastomosantibus; inflorescentia laxe ascendenterque dichotoma corymbosa 3–6 cm. lata multiflora 1–5 cm. longe pedunculata in ramis hornotinis terminali; calyce campanulato ca. 3.5 mm. longo, lobis deltoideis ca. 1 mm. longis nullo modo appendiculatis; corolla alba, 5.5 mm. longa tubulosa; lobis ascendentibus rotundis erosis et crispis saepe ca. 2 mm. longis et 2 mm. latis; tubo ad 2 mm. crasso, intus solum secus nervum infra insertionem staminum positum inconspicue villuloso; staminibus inclusis; filamentis 0.2–0.8 mm. longis 1.7–2.8 mm. supra basim corollae affixis; antheris 1–1.5 mm. longis; stylo 2–2.5 longo calyce vix exserto; endocarpio maturitate subgloboso 3–5 mm. longo.

WEST INDIES. St. Lucia, Dauphin, *P. Beard 1080* (G); Martinique, St. Anne, *Stehlé 6161* (A); Martinique, *Duss 287* (G); Guadeloupe, Anse — Bertrand, *Stehlé 2698* (G), *2689* (G); Marie-Galante, Capesterre, *H. Stehlé 2678* (TYPE, Gray Herb.); Antigua, *Rose, Fitch & Russell 3339* (G); Barbuda, near Codrington Village, *Box 613* (G).

The plant described above is the well known and unmistakable species of the Lesser Antilles which for nearly a century and a half has been

accepted as "*Cordia salvifolia*". The most recent treatment of it is to be found in my account of the "Boraginaceae of the Southern West Indies", Jour. Arn. Arb. 30: 117 (1949). Unhappily, study of the historic specimens at Paris has revealed that the name *C. salvifolia* Juss. ex Poir. Encyc. 7: 46 (1860) applies not to the present species but rather to the very different *Cordia Buchii* Urban (1900), of adjacent southern portions of Haiti and Santo Domingo. Since our plant has no available legitimate name a new one must be proposed.

Cordia (§ Varronia) **lippioides,** sp. nov.

Frutex; ramis hornotinis ca. 10 cm. longis ad 2 mm. crassis hispido-villulosis (pilis 0.5–1 mm. longis); foliis ovatis vel ellipticis 1–2 cm. longis 8–14 mm. latis, basi abrupte acutis in petiolum ca. 2 mm. longum attenuatis, margine crenatis, supra viridibus areolato-bullatis scabris, subtus pallidis nervosis villosis; inflorescentia in ramis terminali vel laterali et oppositifoliata dense hemispherica vel subglobosa 16–20 mm. diametro 15–20-flora 1–2.5 cm. longe pedunculata; calyce sub anthesi 5.5–9 mm. longo supra medium lobato, in alabastro obovato ad 3 mm. crasso apice appendiculas 5 setaceas 1–2 mm. longas liberis terminato; lobis calycis longe subulateque productis, apice setaceis flexuosis hispidulis (pilis saepe brunneis 0.3–0.8 mm. longis); corolla late tubulosa 6.5. mm. longa apice ca. 5 mm. crassa basi ad 2.5 mm. diametro, intus infra insertionem filamentis villulosa, limbo subintegro; filamentis 2–2.5 mm. longis subulatis ca. 3.5 mm. supra basim corollae affixis; stylo 5.5 mm. longo, lobis spathulatis ca. 1 mm. longis; drupa rubra, endocarpio irregulariter elliptico-ovoideo 6 mm. longo 3 mm. crasso.

PERU: Conay, abajo de Chiquián, dept. Ancash, prov. Bolognesi, monte pluvifolio, 2600 m. alt., May 12, 1950, *Emma Cerrate 565* (TYPE, Gray Herb.).

Most closely related to *C. lantanoides* Spreng. (*Varronia crenata* R. & S.), which it closely resembles in foliage and gross habit. It differs from that species, however, in having not only a very much larger calyx but also one in which the lobes have very prolonged tips which are free and flexuous in the bud.

Cordia (§ Varronia) **munda,** sp. nov.

Frutex 12–15 dm. altus; ramis hornotinis 4–10 cm. longis 1–1.5 mm. crassis saepissime simplicibus hispidulo-villulosis (pilis saepe brunneis rectis ascendentibus vel divaricatis 0.5–1 mm. longis); ramis vetustioribus cicatriculas foliorum delapsorum prominulas proferentibus; foliis ovatis vel late lanceolatis 20–45 mm. longis 10–20 mm. latis, apice acutis, basi acutis in petiolum gracilem 2–4 mm. longum contractis, margine crenato-dentatis, supra viridibus pilis rigidulis laxe adpressis vestitis, subtus strigosis; nervis utroque latere costae 5–6 sub angulo ca. 45° abeuntibus curvatis; inflorescentia dense capitata saepe ca. 12 mm. diametro in ramis

terminali graciliter 3–8 cm. longeque pedunculata, calyce 6–7 mm. longo campanulato pilis brunneis 0.5–1 mm. longis gesto, lobis acutis triangularibus valvatis 1.7–2.5 mm. longis; corolla alba conspicua infundibuliformi ca. 25 mm. longa, limbo ascendenti 25–30 mm. diametro, lobis rotundis 7–10 mm. longis, tubo 5–6 mm. longo 2.5–3.5 mm. crasso in zona 1–3 mm. supra basim corollae posita sparse villoso; filamentis subulatis 2–2.5 mm. longis 4.5–6.5 mm. supra basim corollae in altitudinibus diversis affixis, antheris 1.3 mm. longis; stylo 4 mm. longo, lobis 1.5 et 1 mm. longis; fructu ignoto.

PERU: abajo de Aiza, entre Catahuasi y Tupe, dept. Lima, prov. Yauyos, monte subxerófilo, fl. blancas, muy vistosas, 2300 m. alt., Jan. 30, 1952, *Emma Cerrate & O. Tovar 1294* (TYPE, Gray Herb.).

A member of the section Varronia which has an indument of simple (non-stellate) hairs and a terminal inflorescence that is decidedly capitate. The attractive large white infundibuliform corollas have an evidently lobed limb. The calyx-lobes are triangular and have merely an acute apex. The calyx in the bud, accordingly, is rounded on the summit and is not at all terminally appendaged. The species is probably most closely related to *C. Bridgesii* (Fresen.) Johnston, of Bolivia, from which it differs in the much larger, more deeply lobed corollas, the unappendaged calyx, and the larger leaves.

Cordia (§ Varronia) **Vargasii**, sp. nov.

Frutex 15–30 dm. altus; ramis hornotinis 5–25 cm. longis ad 4 mm. crassis velutinis (pilis brunneis 0.5–0.89 mm. longis); ramis annotinis glabratis cicatricis foliorum delapsorum prominentis 1–2 mm. altas proferentibus; foliis ovatis vel ovato-ellipticis paulo asymmetricis 3–10 cm. longis 2.5–5.5 cm. latis, basi obtusis vel rotundis in petiolum 4–6 mm. longum abrupte contractis, apice late acutis, margine evidenter serratis, facie superiore pilis rectis rigidulis 0.4–0.8 mm. longis obsitis, subtus hispidulo-villulosis pallidioribus; nervis primariis foliorum validis aliquando apicem versis furcatis, utroque latere costae 5–7 donatis, nervis secondariis evidentibus numerosis eos primarios conjunctibus; inflorescentia dense capitata 15–23 mm. diametro in ramo hornotino terminali et interdum ex axillis foliorum superiorum rami oriente 2–8 cm. longe pedunculata; calyce anguste campanulato to 5–7 mm. longo apicem versus 4 mm. crasso supra medium pilos brunneos dense proferente in alabastro breviter crasseque apiculato; corolla 5.5–7 mm. longa ut videtur flava tubulosa quam calyce ca. 2 mm. longiore, intus in zona ca. 1 mm. lata infra insertionem staminum posita villosa, basi tubo 1.5–2 mm. crasso, limbo 3–4 mm. crasso, lobis inconspicuis erosis plus minusve rotundis recurvatis ad 1.5 mm. latis et 0.7 mm. longis; filamentis 1.5–2 mm. longis 3–4.5 mm. supra basim corollae affixis; antheris ellipticis ca. 1 mm. longis vix exsertis; stylo aut 2–3 mm. longo et in calyce incluso aut ca. 5 mm. longo et calyce exserto, lobis 0.5–1 mm. longis; fructu ignoto.

PERU (dept. Cuzco): Aobamba, prov. Convención, 1600–1700 m. alt., Nov. 23, 1950, *C. Vargas 9790* (TYPE, Gray Herb.); Amaibamba, prov. Convención, Dec. 29–30, 1948, *C. Vargas 7514* (G); Machupicchu, Oct. 1931, *F. L. Herrera 3227* (G).

This plant has many-flowered, very dense, capitate inflorescences borne on naked peduncles that terminate the leafy stems and sometimes also arise from the upper-most leaf-axils. The leaves are ovate and in form and size are reminiscent of the foliage of *C. spinescens* L. (= *C. ferruginea* Lam.) but differ from it in having petioles which are not decurrent on any subtended peduncle. The closest relationships of *C. Vargasii* appear to be with *C. axillaris* Johnston, of eastern Brazil and the Amazon headwaters of northern Peru (Alto Rio Huallaga, *Klug 4385*). From that species it differs in its ovate (rather than lanceolate) leaves, its less copious indument of shorter hairs, its more elongate, larger calyces, and its prevailingly terminal heads of flowers.

Cordia Gharaf (Forsk.) Ehrenb. ex Asch., Sitzung.-Berichte Ges. Naturf. Freunde Berlin 1879: 46 (1879) & Verhandl. Bot. Verein Brandenb. 21[2]: 69 (1880); Muschler, Manual Fl. Egypt 2: 781 (1912).

Cornus Gharaf Forsk. Fl. Aegypt.-Arab. pg. xcix (1775).
Cornus sanguinea Forsk. Fl. Aegypt.-Arab. 33 (1775), not *Cornus sanguinea* L. (1753).
Cordia sinensis Lam. Tab. Encyc. 1: 423 (1791); Johnston, Journ. Arn. Arb. 32: 11 (1951).
Cordia Rothii R. & S. Syst. 4: 798 (1819).
Cordia subopposita DC. Prodr. 9: 480 (1845).

The identity of *C. sinensis* Lam. (1791) has long remained a mystery and there are numerous guesses recorded in the literature as to what species and genus it might represent. During a recent visit to Paris I took the opportunity to examine the type specimen in Lamarck's herbarium. Much to my surprise I found the plant to be the very distinctive desert shrub, *Cordia Gharaf* (Forsk.) Ehrenb., which occurs in Pakistan and western India and also in the deserts of Arabia and eastern Africa. The eastern form of the species, that found in India and Pakistan, was formerly distinguished as *Cordia Rothii* R. & S. The plant does not grow in China nor is it to be expected there. The geographic data associated with the type of *Cordia sinensis* Lam. are accordingly false and misleading. Sonnerat, the collector of the type, must have found the plant in western India.

The name *Cordia Gharaf* currently appears to be generally accepted as the proper name for the present species. Its claims for acceptance, however, are somewhat questionable. The basionym, *Cornus Gharaf*, was not described by Forskål. It is mentioned six times (on pages xci, xciii, xcv, xcvi, xcvii and xcix) in the prefatory portions of his book concerned with the plants of Yemen and there only as a name in lists of economic plants. It is always a bare name except on pg. xcix where, in a list of medical

plants, it is given as follows: "*CORNUS gharaf*. C. II. 10. In cephalalgia." The symbols (C. II. 10.) refer to Centuria II, species no. 10, or in other words to the main body of Forskål's book in which species are described and given individual treatment. The particular reference is to the account of *Cornus sanguinea* of pg. 33. *Cornus sanguinea* Forsk. and the nomen nudum *Cornus Gharaf* Forsk., are alternate equivalent names for one and the same species. The reference on pg. xcix is evidence of this. Indicative also is the fact that all the economic uses attributed in various lists to *Cornus Gharaf* are all mentioned again in the paragraph in which *Cornus sanguinea* is described and its properties enumerated. Although the binomial *C. Gharaf* is not cited as a synonym in the account of *S. sanguinea*, the vernacular "gharaf" is given as a name applied to the plant at Hodeida, Yemen. It seems likely that the binomial *Cornus Gharaf* was intended as only a temporary appellation, perhaps for use by Forskal during his field work. Although used in his notes, it was one which he subsequently planned to replace with the name *Cornus sanguinea*. In the posthumous editing of his manuscripts by Niebuhr, the preliminary name was not altered, with the result that two names for the species were published.

The two binomials published in Forskål's "Flora Aegyptiaco-Arabica" are the oldest ones applied to the Cordia in which we are interested. Of these, *Cornus sanguinea* Forsk. (1775) is a later homonym of *Cornus sanguinea* L. (1753) and must be rejected. Being illegitimate it can not serve as a basionym and the specific epithet is not available for transfer to *Cordia*. Accordingly only *Cornus Gharaf* Forsk. is available as a possible basis for a binomial combination under *Cordia*. As I have indicated, even the validity of this name is open to possible challenge. A case against its acceptance can be made on the grounds that obviously it is a temporary, provisional or alternative name which the author did not intend to retain and would not have published had he lived to edit and publish his own manuscript. Nevertheless the binomial actually is published and on pg. xcix of Forskål's book is associated with a description of a plant printed on pg. 33 of the same volume. The minimum requirements for valid publication of the name *Cornus Gharaf* seem to be fulfilled. This is desirable, for otherwise *Cordia Gharaf* (Forsk.) Asch. would not be the valid correct name for our plant and the obscure, long-confused species with the inappropriate name *Cordia sinensis* Lam. would have to be accepted in its stead.

Bourreria Rowellii, sp. nov.

Arbor ad 4–5 m. alta; foliis oblanceolatis 5–7 cm. longis 16–22 mm. latis nervosis (nervis ramosis utroque lateris costae 5–8) supra medium latioribus deinde deorsum gradatim attenuatis, basi acutis, apice obtusis, facie superiore glabris vel solum secus costam sulcatam sparsissime inconspicuissimeque villulosis, facie inferiore pallidioribus leviter appresso-villulosis (pilulis gracillimis 0.2–0.5 mm. longis), margine anguste revolutis; petiolo gracili 0.3–0.6 mm. longo; inflorescentia terminali laxe

cymosa 3–5 cm. diametro 6–12-flora; calyce 7–8 mm. longo, tube 4–4.5 mm. diametro basi rotundo sessili, lobis triangularibus acutis erectis ca. 3 mm. longis et 2.5 mm. latis, extus griseis minute villulosis, intus albis dense strigosis; corolla alba infundibuliformi ad 17 mm. longa a basi 3 mm. crassa sursum gradatim expansa, limbo 15–18 mm. diametro, lobis ascendentibus rotundis 5–7 mm. diametro extus sparse inconspicueque stipitato-glanduliferis et secus nervum medialem pilos paucos albos adpressos ad 1 mm. longos proferentibus; filamentis attenuatis ca. 8 mm. longis stipitato-glanduliferis nullo modo villulosis ca. 4.5 mm. supra basim corollae affixis apice basim sinuum limbi corollae 1–2 mm. longe superantibus; antheris 3 mm. longis; granulis pollinis 3-colpatis a latere visis transverse ellipticis 65 μ latis 50 μ altis, desuper visis circularibus vel plus minusve triangularibus 65 μ latis; stylo glaberrimo 10–12 mm. longo apice 2–3 mm. profunde bilobato; fructu ignoto.

MEXICO: rocky limestone hillside 1 mile west of Colotlipa, Guerrero, 2700 ft., tree 15 ft. tall with white flowers, June 24, 1953, *Chester M. Rowell, Jr. & H. D. Irby 3545* (TYPE, Arn. Arb.).

An arborescent species with funnelform corollas, ascending corolla-lobes and non-exserted stamens. Its relatively small, oblanceolate leaves are neither pustulate nor hairy on the upper surface. The plant grows in the same region as *Bourreria spathulata* (Miers) Hemsl. The latter is readily distinguished by having widely spreading corolla-lobes, conspicuously protrudent villulose, as well as glanduliferous filaments, and smaller leaves with few evident veins and a short-strigose, usually pustulate upper leaf-face. The closest relation of *B. Rowellii* is probably *B. Hintonii* Johnston of coastal Guerrero. The latter has scabrous upper leaf-surfaces but otherwise the plant is practically glabrous. Its calyx is narrower and the calyx-lobes more slender and its filaments completely glabrous, bearing neither hairs nor stipitate glands.

Tournefortia Romeroi, sp. nov.

Frutex 2 m. altus velutinus; ramis hornotinis fistulosis ad 0.9 mm. crassis dense velutinis (pilis ca. 1 mm. longis abundantissimis); foliis elliptico-lanceolatis 12–25 cm. longis 5–9 cm. latis, apice graciliter longeque attenuatis, basi acutis in petiolum 10–20 mm. longum 2–3 mm. crassum velutinum attenuatis, margine inconspicue minuteque denticulatis, supra sparse velutinis (pilis ca. 0.5 mm. longis erectis solum in aerolis nervorum crebris secus nervos ipsos carentibus); subtus pallidioribus dense velutinis (pilis ca. 1 mm. longis gracillimis solum secus costam et nervos gestis); nervis laminae folii primariis utroque latere costae 12–15 arcuatis, eis secondariis tertiariisque reticulato-anastomosantibus in facie superiore folii areolas minutas 0.5–1.0 mm. latas numerosissimas circumscribentibus; inflorescentia e axillaribus foliorum superiorum orienti pendula 5–7 cm. longe pedunculata dichotoma, ramis duobus simplicibus 5–10 cm. longis vel eis iterum ramosis; calyce sessili, lobis conspicue inaequalibus gracilli-

mis subulatis supra medium non rariter recurvatis basim versus 0.4–0.6 mm. latis, lobo majore 7–8 mm. longo, minore 4–6 mm. longo; corolla pallide viridi 10–12 mm. longa, extus pilulis 0.1–0.2 mm. longis sparse obsita, intus glaberrima, tubo elongato infra medium 0.5–1.0 mm. crasso, apicem versus crassisimo in faucis 2–3 mm. longos 1.5–2.5 mm. crassos expanso, lobis ascendentibus lanceolatis vel oblongis acuminatis 1.8–2 mm. longis 0.8–1.5 mm. latis; antheris oblongis ca. 0.7 mm. longis supra basim affixis; filamentis perbrevibus 0.1–0.2 mm. longis ca. 1 mm. infra basim loborum corollae insertis; ovario glabro sub anthesi angusto ovoideo ca. 1 mm. longo stylum glabrum 4–6 mm. longum proferenti; stigmate annulum ca. 0.5 mm. diametro gerenti, apice appendiculam sterilem 0.3–0.5 mm. longam subconicam proferenti; fructu ignoto.

COLOMBIA: La Guayacana (Tumaco), dept. Nariño, shrub 2m. tall, inflorescence pendant, sepals green, corolla pale green, lobes on face pale salmon-color in age, ovary green globose-oblong, June 24, 1951, *R. Romero-Castañeda 2837* (G); El Diviso, Km. 86 F.C. Tumaco, dept. Nariño, shrub 2 m., inflorescence pendulous; corolla pale green, the lobes pale salmon in age, sepals green, "oreja de macho," July 27, 1952, *R. Romero-Castañeda 3317* (TYPE, Arn. Arb.).

A very well marked species notable for its velvety indument, the pendulous inflorescence, the very slender and elongate sepals, and the slender elongate corollas. The two collections studied are dark from a very dense velvety indument decidedly brown in color. It is not known if this color is present in the living plant or if it is assumed by the plant in drying.

Associated with this new species from southwestern Colombia, is the name of the collector, Rafael Romero-Castañeda, of the Ministerio de Agriculture, Bogota. Sr. Romero-Castañeda has sent me various lots of Boraginaceae collected during his travels about Colombia. It is fitting that his name should be associated with one of his most attractive discoveries.

Tournefortia microcalyx (R. & P.), comb. nov.

Heliotropium microcalyx R. & P. Fl. Peruv. **2**: 3, t. 109b (1799).
Tournefortia obtusiflora Benth. Bot. Voy. Sulphur 140 (1845).

Over 25 years ago, Contr. Gray Herb. **81**: 72 (1928), after study of authentic material, I indicated that the species of Ruiz & Pavon was properly classified as a species of *Tournefortia*, but by some mischance the new name required in transfering it to Tournefortia was never published. The plant concerned is a readily recognizable one apparently common in a large area in the province of Lima, Peru. Although the source of the type-collection was originally given as "in Peruviae collibus per Huanuci Provinciam", I have collections of the species only from west of the high mountains. It apparently ranges from the Lima area northward on the Pacific slope into southern Eucuador.

Heliotropium Ferreyrae, sp. nov.

Frutex 6–8 dm. altus; ramis numerosis gracillimis 1–2 mm. crassis ascendenter ramosis inconspicue strigulosis (pilis vix abundantibus gracillimis valde adpressis rectis 0.2–0.8 mm. longis); foliis abundantibus non rariter fasciculatis 2–5 cm. longis 1–5 mm. latis, supra medium latioribus deinde deorsum in basim subpetiolatam gradatim longeque attenuatis, apice gradatim attenuatis, supra strigulosis (pilis 0.2–0.5 mm. longis) costa profunde sulcata donatis, subtus pallidis pilis 0.2–1.0 mm. longis vestitis costa prominenti donatis; cymis caulem ramosque terminantibus ebracteatis geminatis ternatisve gracillimis multifloribus 5–25 cm. longis solum ad apicem scorpioideis; floribus numerosis sub anthesi congestis, fructiferis 5–15 mm. distantibus; calyce ad anthesin 2 mm., longo pentifido, lobis inaequalibus anguste lanceolatis tubo corollae subaequilongis; calyce fructifero vix accrescenti 0–1 mm. longe pedicellato; corolla alba 2.3–2.7 mm. longa; tubo corollae subcylindrico 1.5–1.7 mm. longo ca. 1 mm. crasso, extus strigoso, intus secus venas infra lobos corollae positas minute albo-hispidulo alibi glabro; limbo corollae 2–2.2 mm. diametro, lobis recurvatis triangularibus ca. 0.7 mm. longis; sinibus limbi basi truncatis inflexo-plicatis; antheris elongatis haud cohaerentibus subsessilibus 0.8 longis ad 0.2 mm. latis ad 0.8 mm. supra basim corollae basifixis, apice rotundis nec appendiculatas nec pilas evidentis gerentibus; stigmate subsessili elongato sursum angustato ad 0.8 mm. longo basi annulo ad 0.25 mm. diametro donato, apice angusto ad 0.15 mm. crasso saepe obscure emarginato; fructu ca. 1.5 mm. alto ca. 2 mm. lato 4-lobato apice obtuso stigmatem sessilem gerente; nuculis 4 dorse convexis et strigosis, ventre angulatis.

PERU (Prov. Piura): 100 km. south of Piura, shrub 6–8 dm. tall, sandy pampa, 250–300 m. alt., fl. white, May 2, 1949, *Ramón Ferreyra 6044* (TYPE, Arn. Arb.).

A species most closely related to *Heliotropium polyanthellum* Johnston of northern Peru but quickly distinguishable from it by having lines of hairs in the corolla-throat and by having a subsessile stigma. In the related species the corolla-throat is glabrous and the stigma is borne on a style 0.2–0.3 mm. long. The proposed species has other characters in its scanty indument, very slender and elongate loosely branched stems, greatly elongating cymes, and small corolla with proportionately shorter tube.

Coldenia Ferreyrae, sp. nov.

Frutex prostratus glanduliferus dichotome ramosus; caulibus 1–5 dm. longis nodosis faciliter disarticulatis, internodis 1–5 cm. longis 1–4 mm. crassis juventate hispidulis et stipitato-glanduliferis, maturitate cortice chartacea decidua donatis; foliis ad nodos caulis aggregatis; lamina crassiuscula strigosa vel adpresse hispidulo-villulosa et sparse glandulifera,

elliptica 0.8–1.5 cm. longa 3–5 mm. lata utroque acuta, basi in petiolum gracilem villosum glanduliferum 3–5 mm. longum attenuata, supra utrinque lateribus costae sulcatae nervis 2–4 sulcatis donata, subtus costa et nervis latis prominulis donatis, margine revoluta; floribus glomeratis; calyce sessili 5–6 mm. longo, lobis sub anthesi subulatis villuloso-hispidulis et glanduliferis tubum corollae breviter superantibus, tubo calycis fructiferi evidenter 5–costato, costis prominenter suberoso-encrassatis; corrolla alba infundibuliformi glaberrima 9–11 mm. longa, tubo cylindrico ca. 4.5 mm. longo et ca. 1 mm. crasso, limbo 5–7 mm. diametro, lobis ascendentibus obovatis ca. 3 mm. longis 2–2.3 mm. latis; filamentis filiformibus 4–7 mm. longis evidenter exsertis, in faucibus 5–6 mm. supra basim corollae insertis, infra insertionem deorsum secus costam invaginatam tubi corallae 2–3 mm. longe decurrentibus (tubo corollae infra basibus decurrentibus filamentorum nullo modo appendiculato); antheris ca. 1.0 mm. longis; pollinis desuper visis ca. 33 μ latis plus minusve trilateralibus, a latere visis quadratis 33 x 41 μ poris 3; stylo filiformi 11–14 mm. longo apicem versus furcato, lobis 0.5–1 mm. longis, stigmatibus minutis; ovulis 4; nuculis saepe 2, 1.3–1.5 mm. longis, dorse alte convexis dense minutissimeque papillatis, ventre planis, margine angulatis sed nullo mode alatis.

PERU: (dept. Arequipa): betw. Nazca and Chala, Km. 545–46, Alt. 200 m., fl. white, Nov. 7, 1947, *R. Ferreyra 2506* (TYPE, Arn. Arb.); vicinity of Camaná, 20–30 m. alt., in sand, fl. white, *Ferreyra 2550* (G); Lomas de Camaná, 180–200 m., sand, fl. white, *Ferreyra 8847* (A); Rio de Lomas, Acaré, 800–900 m. alt., *Weberbauer 5734* (G).

A very well marked species readily distinguished from all other South American congeners by having the lobes of the fruiting calyx conspicuously thickened with corky ribs below the middle. The closest relation of the plant is the habitally similar *Coldenia simulans*, which comes from the same floristic area in coastal southern Peru. This latter species may be distinguished from *C. Ferreyrae* by the lobulate appendages which are well developed inside its corolla-tube, a pair being located about 1 mm. below the attachment of each stamen. These appendages, well developed also in *C. dichotoma*, are absent from the corolla of *C. Ferreyrae*. In all the three species mentioned the inner surface of the corolla-tube is ridged for 1–3 mm. directly below the attachment of each of the stamens. The ridges, although readily mistaken for thickened decurrent bases of the filaments, are actually formed by invagination, each of the ridges on the inside of the tube having a complement in a narrow, elongate depression at the same relative position on the outside of the tube. The vein leading to the stamen passes along the summit of the invaginate ridge but along the ridge the vein is not associated with an appendage. Below the invagination, however, there may be knife-like downwardly elongate appendages close to and paralleling the vein on left and right. In *C. simulans* and *C. dichotoma* the bialate appendage associated with the vein is conspicuously well developed just below the invagination, and is there decidedly lobulate and crisped. In *C. Ferreyrae* the appendages accompanying the veins are

obscure and at best very narow and sometimes are even absent. Their presence or absence can be determined only by examination of the corolla under very high magnification. They are never enlarged, nor crisped, as is the case in both *C. simulans* and *C. dichotoma*.

The South American species are not separable by marked differences in pollen. The grains from species to species differ only slightly in size and form. In polar profile, though sometimes nearly circular, they tend to be more or less definitely three-sided with the angles broadly rounded. There are three pores. In lateral profile the grains are more or less quadrate in outline and are slightly to very evidently longer than broad. Viewed laterally the polar ends are broadly rounded while the sides are nearly straight and parallel. They measure 30–47 μ in length along the polar axis and 26–33 μ broad at the equator. The smallest average size occurs in *C. dichotoma* (26 x 30 μ) and the largest in *C. grandiflora* (33 x 47 μ). Pollen of the North American species has not been examined. The pollen of the Old World *C. procumbens* L., however, though showing general similarities with the *Coldenia* pollen examined, does differ in a number of notable respects. It has three pores and is also three sided in polar profile, but in lateral view is distinctly elliptic and is very much broader than long, being 25 μ in length along the polar axis and 33μ broad at the equator. Unlike the pollen of the South American species, that of *C. procumbens* has a surface not practically smooth, but one that appears distinctly granulate.

Coldenia simulans, sp. nov.

Frutex prostratus glanduliferus dichotomus ramosissimus; caulibus 1–5 dm. longis nodosis faciliter disarticulatis, internodis 1–5 cm. longis 1–4 mm. crassis, juventate hispidulis et stipitato-glanduliferis, maturitate cortice chartacea decidua donatis; foliis ad nodos caulis aggregatis; lamina crassiuscula ovato vel lanceo-ovato acuta 7–14 mm. longa 3–5 mm. lata, supra strigosa utrinque lateribus costae nervis 2–3 sulcatis donata, subtus prominenter nervosa villulosa secus costam glandulifera, margine valde revoluta; petiolo 2–4 mm. longo glandulifero; floribus glomeratis; calyce sessili 3–4 mm. longo, lobis lanceolatis acutis villulosis tubo corollae subaequilongis; corolla alba infundibuliformi glabra 4.5–6 mm. longa, lobis ascendentibus obovatis ca. 2 mm. longis et 1 mm. latis, tubo cylindrico ca. 3 mm. longo et 1–1.3 mm. crasso summum ad apicem filamenta proferente infra insertionis filamentorum costis invaginatis ad 1 mm. longis donato, basibus costarum (i.e. ca. 2 mm. supra basim corollae) appendiculis bialatis lobatis et crispis praedito; filamentis filiformibus inaequalibus 4–5 mm. longis evidenter exsertis 3–3.5 mm. supra basim corollae insertis; antheris 0.8–1.1 mm. longis; stylo ca. 7 mm. longo, apice ca. 1 mm. profunde lineariter bilobato; nuculis 2–2.3 mm. longis 1.0–1.3 mm. latis plano-convexis.

PERU (dept. Arequipa): El Jagüay, Km. 538, fl. white, Aug. 22, 1948. *Rosa Scolnik 1010* (TYPE, Arn. Arb.); Puerto de Lomas, Oct. 3, 1931. *Father Jaffuel 2137* (G); Puerto de Lomas, *Weberbauer 5730* (G).

Closely related to *Coldenia dichotoma* and perhaps only a very well developed geographic variation differing in its small leaves and less evident conspicuously fewer veins. Whereas *C. dichotoma* has been found at various stations along the Peruvian coast from Lima north to Talara. *C. simulans* is known only from a limited area of coastal southern Peru lying just south of the Ica-Arequipa departmental boundary.

The Peruvian species of *Coldenia* all show a preference for sandy soil. Indeed, most of them are restricted to dunes, especially those near the ocean. Although proper ecological conditions appear to be almost continuously present along the length of the Peruvian coast, only one species of *Coldenia* ranges along more than half of it. *Coldenia parviflora* and *C. grandiflora* are known in Peru only from the interior, from sandy places and dunes near the city of Arequipa. *Coldenia conspicua* and *C. litoralis* are known from Peru only from the south coast, from Mollendo southward. *Coldenia Ferreyrae* and *C. simulans* are known only from a short section of coast between Mollendo and Lima. *Coldenia dichotoma* is known only from the Peruvian coast from Lima northward. The most widely distributed species, occurring along the coast and also well back from the coast, and in southern as well as in northern Peru, is *C. paronychioides*. Of the eight species known from Peru, five are endemic to the country; three (*C. grandiflora*, *C. litoralis*, *C. paronychioides*) extend well southward into Chile; and only *C. paronychioides* reaches into Ecuador. Only two, *C. dichotoma* and *C. paronychioides*, occur about Lima and northward. The six other Peruvian species all reach their northern limit further south. The eight species of *Coldenia* known from Peru may be distinguished by the following key:

Nutlets distinctly plano-convex, with a high rounded back and a broad flat commisural face; stamens usually evidently exserted from the corolla.
Corolla blue; nutlets with knife-like lateral margins, known from the vicinity of Arequipa (1800–2200 m. alt.) and south into northern Chile. ..... *C. grandiflora* Phil.
Corolla white or very pale bluish; nutlets with angled but not knife-like margins.
Fruiting calyx developing prominent corky-thickened ribs; corolla-tube not appendaged a short distance below the attachment of the filaments; plant of coastal southern Peru, 20–900 m. alt. . *C. Ferreyrae*, sp. nov.
Fruiting calyx without corky-thickened ribs; corolla-tube bearing a pair of crisped lobulate appendages a short distance below the attachment of each filament.
Leaves bearing 4 to 6 well developed veins on each side of the midrib; plant of coastal Peru north of Lima, 0–50 m. alt. ..... *C. dichotoma* (R. & P.) Lehm.
Leaves bearing only 2 to 3 veins on either side of midrib; plant of coastal southern Peru. ..... *C. simulans*, sp. nov.

Nutlets not conspicuously flattened on the ventral (commisural) side, more or less sphaerical or lance-oblong in form, not distinctly plano-convex; stamens included and equal or nearly so.

Attachment-scar narrow, elongate, longitudinal on the lance-oblong nutlets; corolla very small 2.5–3.5 mm. long; ranging from northern Chile to Ecuador, along the coast and in the interior, 0–2300 m. alt. . . . . *C. paronychioides* Phil.

Attachment-scar small, localized on one side of the nearly sphaerical nutlet; corolla larger, over 7 mm. long.

Corolla 11–16 mm. long; calyx 8–13 mm. long, glanduliferous; nutlets 1.2–1.5 mm. in diameter, with a very prominent bony convex commisural surface; coast of southern Peru (Mollendo, Mejia, Cachendo), 0–1000 m. alt. . . . . *C. conspicua* Johnston

Corolla 7–9 mm. long; calyx 2.5–5 mm. long, not glanduliferous or only very sparsely so; nutlets 1 mm. or less in diameter, commisure not very prominent.

Leaves lanceolate, largest ones 8–17 mm. long, sharply acute, with 3–5 veins on each side of midrib; region about Arequipa, 2200–3400 m. alt. . . . . *C. elongata* Rusby

Leaves ovate or elliptic, largest one 5–10 mm. long, usually obtuse, 2–3 veins on each side of the midrib; coast of southern Peru (Mollendo, Mejia, Tacna) and south into Chile where it is the most common and wide-spread speceis. . . . . *C. litoralis* Phil.

Onosma brachylinum (Johnston), comb. nov.

Onosma Waddellii var. *brachylinum* Johnston, Jour. Arn. Arb. **32**: 345 (1951).

Plant annual or biennial; stems one to several 1–3 dm. long 1.5–3.5 mm. thick, decumbent to erect, usually ascendingly branched, pungently hispid with spreading hairs 1–3 mm. long; leaves veinless or nearly so, all cauline, numerous, green, usually paler beneath, upper surface in age frequently dotted with discoid hair-bases, hispid with straight stiff erect or ascending hairs 1–3 mm. long; lowest leaves largest and more or less oblanceolate, 3–7 cm. long, 8–13 mm. broad; middle leaves 2–4 cm. long, 4–8 mm. broad, sessile; basal leaves not persisting at flowering time; cymes terminal on the main stem and branches and frequently pedunculate in the upper leaf-axils, frequently forked, at anthesis dense, 1.5–2.5 cm. in diameter, remaining congested even in fruit; calyx 5–8 mm. long, weakly accrescent at maturity, lobes hispid, pedicel 1–3(–5) mm. long; corolla usually pink but sometimes blue or white, 11–13 mm. long, with a short tube ca. 2 mm. thick then expanding into a campanulate throat becoming 5–8 mm. in diameter, outside usually inconspicuously strigulose or hispidulous on and below the lobes, inside glabrous except for the usually villulose annulus; corolla-lobes triangular 1–1.5 mm. long, 2–3 mm. broad, margins revolute; anthers 4.5–6 mm. long, coherent at the base and along the sides to form a tube, affixed ca. 1.5 mm. above the base, included or with only the sterile tip exserted, sterile tip 0.4–0.9 mm. long; filaments 2.5 mm. long, arising 3–4.5 mm. above the corolla-base, decurrent base 2–3 mm. long; annulus very narrow, 0.3 mm. high, villulose lobulate; style

glabrous, commonly exserted 1–2 mm.; nutlets 2–2.5 mm. long olivaceous, somewhat lustrous, sparsely pappillate and obscurely rugulose.

TIBET: Kyimpu, Chayul — Charme road, among shrubs on stony hillside in warm valley, 12,000 ft., corolla mostly bright reddish pink, some colored blue, July 26, 1936, *Ludlow & Sherriff 2440* (BM); Trün, Chayul Chen, on rocky open hillside, dry valley, only one plant seen, corolla pink, 11,500 ft., July 22, 1936, *Ludlow & Sherriff 2418* (BM); Sanga Chöling, Charme, dry stony scrub-covered slopes facing south, not common, plentiful in certain spots, 11,000 ft., Sept. 18, 1935, *Kingdon-Ward 12355* and *12355A* (BM); Kyimdong Dzong, Tsangpo Valley, fl. white, stony screes in rocky gorge, 11,000 ft., July 14, 1935, *Kingdon-Ward 11991* (BM); Kharkhung, 12,500 ft., June 23, 1936, *N. Humphreys 5026* (BM).

This plant was previously known to me only from some collections from the Tibetan valleys north of Mt. Everest. The collections cited above come from regions farther east, from the area north of eastern Bhutan. The species is now known to range along the north side of the Himalaya in southern Tibet between long. 87° and 94° E.

Although probably most closely related to *Onosma Waddellii* Duthie, a species of the dry sands and gravels along the Tsangpo Valley, the present plant is readily distinguished from its relative by its looser, more branching habit, its spreading pungent indument, and its included anthers and short (2–3 mm., not 5–7 mm. long) filaments. It is a plant of stony slopes and hillsides. Its corollas are pink or become blue in age, but never achieve the bright blue which is one of the distinguishing features of *O. Waddellii*.

Maharanga bhutanica, sp. nov.

Planta perennis e radice valida palari 5–10 mm. crassa erumpens; caulibus pluribus 1–2 dm. longis simplicibus ascendentibus 1–2 mm. crassis pilis gracilibus patentibus 2–3 mm. longis rigidulis abundante donatis; foliis firmiusculis costa et nervis evidenter donatis adpresse hispidis (pilis rectis abundantibus 2–4 mm. longis) et praesertim in facie inferiore minute inconspicueque strigosis (pilulis 0.1–0.5 mm. longis), maturitate facie superiore basis pallidas discoideas pilorum notatis; foliis basalibus persistentibus 5–9 cm. longis 1–2 cm. latis utroque acutis; nervis utrinque lateribus costae 3–4 validis assurgentibus in facie superiore sulcatis in facie inferiore prominulis; foliis caulinis parvis lanceolatis 1–3 cm. longis 4–8 mm. latis inferioribus quam superioribus aliquandum majoribus vel plus minusve equalibus; cymis terminalibus densis sub anthesi 2–3 cm. diametro; calyce hispido sub anthesi 4–5 mm. longo fere ad medium lobato, lobis triangularibus acutis; corolla caerulea 9–11 mm. longa, base imma 1.5 mm. crassa, medium versus 4–5 mm. crassa, ore 1–2.5 mm. diametro, extus strigulosis (pilulis 0.1–0.3 mm. longis retrorsis antrorsisque) a fundo sinum usque ad medium tubi 5-sulcata, infra medium tubi costis 5 inflatis et areolis 3 planis ellipticis apice haud invaginatis ornato, intus solum in annulo fere ad 1 mm. alto villulosa alibi glabra; antheris 4–

4.5 mm. longis basi coherentibus inclusis 1 mm. supra basim affixis, apicibus sterilibus denticulatis ca. 0.8 mm. longis, basibus 4–5 mm. infra sinus corollae positis; filamentis 2–2.5 mm. longis, sursum gradatim attenuatis 3.5–4 mm. supra basim corollae affixis; stylo glabro; nuculis ignotis.

BHUTAN: Chungkar, common on cliff-ledges, 7000 ft. alt., corolla blue, pink when first opening, June 6, 1947, *F. Ludlow, G. Sherriff & H. H. Elliot 12598* (TYPE, Brit. Mus.).

This species is a coarse perennial and has the gross habit of *Maharanga emodi* (Wall.) DC. It works out to the latter species in my key to plants of this relationship, Jour. Arn. Arb. 32: 206 (1951). The Bhutan plant differs from *M. emodi* in being much more abundantly hairy and in having elongate corollas, reduced cauline leaves, and conspicuously veined, more persistent basal leaves. In *M. emodi* the cauline are gradually larger upward along the stem, with the lowest imperfectly developed and those below the cyme largest and best developed. In *M. bhutanica* the cauline leaves are all about equally developed with the lowermost only very slightly larger than the uppermost. The proposed new species is known only from relatively low altitudes in Bhutan, whereas *M. emodi* occurs between 10,000 and 15,000 ft. alt. and ranges from Bhutan to Kumaon.

Maharanga emodi (Wall.) DC., var. **stelligera,** var. nov.

A var. typica differt foliis basalibus in utrinque lateris et foliis caulinis in facie inferiore pilis stellatis abundantibus gestis; pilis majoribus 3–6 mm. longis e centro disciformi pallidi erumpentibus, basi pilulos ca. 1 mm. longos pluros radiate dispositos disco pallido marginem versus erumpentes circumdatis.

BHUTAN: Tang Chen, Ritang, corolla blue-violet to purple-blue, lobes bright red or reddish blue, on cliff ledges and on steep open slopes among stones, 12,000 ft., *F. Ludlow & G. Sherriff 3234* (TYPE, Brit. Mus.; ISOTYPE Arn. Arb.).

In this plant the basal leaves are pallid with an appressed villose-hispid indument composed solely of stellate hair-clusters. The cauline leaves, however, are green and their sparse indument contains stellate hair-clusters only on their lower surface. Hair clusters of a similar sort occur in two other species of *Maharanga*, *M. egregia* Johnston and *M. Wallichiana* DC.

Craniospermum echioides (Schrenk) Bunge, Heliocarya 10 (1871).

Diploloma echioides Schrenk, Bull. phys.-math. Acad. Petersb. 2: 195 (1844).
Craniospermum mongolicum Johnston, Jour. Arn. Arb. 33: 74 (1952).

DZUNGARIA: Ala-tua, 1840, *A. Schrenk* (Paris, ISOTYPE of *D. echioides*).
MONGOLIA: Daying Gol, *Chaney 195* (G, TYPE of *C. mongolicum*).

I have examined the authentic specimens of *Craniospermum echioides*, from the herbarium of Bunge, now preserved at Paris. It is without any doubt conspecific with the type of *C. mongolicum*. The plant involved

appears to be extremely rare and at present is known only from the two localities cited. These two stations both lie near lat. 45° N. but are separated from west to east by over 1500 kilometers.

Brand, Pflanzenr. Heft 97: 103 (1931), apparently saw no material of *C. echioides*, for he lists the species as a synonym of the very different *C. subvillosum* Lehm. Actually the species is not very closely related to the other species of *Craniospermum* and, if it is not eventually separated from them to form the monotypic genus *Diploloma*, it should be segregated within in *Craniospermum* to form the section Diploloma, as Popov, Fl. URSS 19: 535 (1953), has recently done.

The pollen of *C. echioides* is sphaerical and 33–39 μ in diameter. It bears three broad granular elliptic areas, usually more or less protrudent, equally spaced about the equator. I am unable to distinguish it by size or form from the pollen of other members of the genus. The pollen from the type specimen of *C. mongolicum* is mostly imperfect and not characteristic. It is smaller (at most 25 μ in diameter) than in other collections but otherwise similar.

Hackelia Stewartii, sp. nov.

Planta herbacea perennis 6–10 dm. alta; caulibus erectis fistulosis basim versus ad 8 mm. crassis, apicem versus ramulos paucos ascendentis floriferos 5–20 cm. longos gerentibus; foliis caulinis lanceolatis; lamina 6–18 cm. longa 2 — 8 cm. lata, basi acuta vel plus minusve obtusa in petiolum 5–35 mm. longum contracta, apice graciliter attenuata, facie inferiore pallidiore villulosa pilulis mollibus 0.1–0.5 mm. longis vix abundantibus vestita, facie superiore viridi scabrella pilulis gracilibus inconspicuis adpressis 0.1–0.6 mm. longis obsita; nervis lateralibus laminae evidentibus, eis in tertia parte inferiore costae orientibus conspicue longissimis fere ad apicem folii attingentibus; cymis solitariis vel geminatis in caulibus et ramulis terminalibus 7–15 cm. longis ebracteatis vel basim versus bracteas saepe solitariis foliatas 1–4 mm. longas gerentibus; calyce pallido dense villuloso, lobis acutis ad anthesin cuneato-lanceolatis 1.5–2.5 mm. longis 0.6–1.0 mm. latis, in statu fructifero plus minusve ovatis ad 3.5 mm. longis et 2 mm. latis; corolla pallide azurea 10–14 mm. diametro, tubo 1.5–2 mm. longo, lobis rotundis patentibus ad 4 mm. diametro; appendiculis faucium exsertis oblongis 1–1.3 mm. longis 0.8–1 mm. latis marginibus lateralibus villosis; nuculis marginatis dorse non rariter inconspicue hispidulis; corpore nuculae 4.5–5 mm. longo 2–3 mm. lato, margine saepe alato, ala 0.3–2 mm. lata appendiculas uniseriatas subulatas glochidiatas 1–3 mm. longas armatos; gynobasi 2.5–3 mm. longa basi ca. 2 mm. crassa; stylo elongato 2–2.5 mm. longo maturitate saepe exserto.

KASHMIR: Rajdhiangan Pass, fl. pale blue, July 19, 1940, *R. R. Stewart 19526* (TYPE, Gray Herb.); trip to Gurais, May–June, 1929, *R. R. Stewart 12955* (G); Sonamarg, 11,000 ft., fl. light blue, July 18, 1928, *R. R. Stewart 12959* (G); Killanmarg, 10,000 ft., Aug. 1926, *R. R. Stewart 8604A* (G); Pahlgam, 10,000

ft., Aug. 8, 1927, *R. R. Stewart 12956* (G); mountains opposite Pahlgam, 11,000 ft., fl. pale blue, Aug. 28, 1945, *R. R. Stewart 21816* (G); Zur Nar above Arie, Liddar Valley, fl. large and dark, usually sky blue, half inch in diameter, Aug. 3, 1945, *R. R. Stewart 21563* (G); 6 mi. south of Karagbal, fir forest, 8000 ft., plant 3 ft. tall, fl. sky blue, Aug. 1, 1936, *W. Koelz 9239* (G).

A readily recognizable species which appears to be most closely related to *Hackelia uncinata*, the most widely distributed member of the genus in the western Himalaya. In gross habit it is intermediate between that of *H. uncinata* and *H. macrophylla*. Both of these latter species range in same general area as that in which *H. Stewartii* is found. The proposed species may be distinguished from the other Himalayan species of the genus by the following key:

Upper leaf-face more or less lustrous, glabrous or nearly so; corolla 10–15 mm. in diameter, white or white with a blue or purple spot between the bases of the lobes; nutlets bearing glochidiate appendages on the dorsal surface as well as on the margin; Kashmir and adjacent Punjab. . . . . *Hackelia macrophylla* (Brand) Johnston.

Upper leaf-face with abundant minute appressed hairs, not lustrous; corolla pale to dark blue; nutlets not bearing glochidiate appendages on the dorsum, bearing them only on the margin.

Style elongate, 2–2.5 mm. long; corolla large, 10–14 mm. in diameter, pale blue, faucal appendages longer than broad, 1–1.3 mm. long, ca. 0.8 mm. broad; stem leaves large, broadly lanceolate, 6–18 cm. long, 2–8 cm. broad, lower ones not cordate; Kashmir. . . . . *Hackelia Stewartii*, sp. nov.

Style short, 0.2–0.8 mm. long; corolla usually less than 10 mm. in diameter, faucal appendages usually broader than long, 0.3–0.8 mm. long and 0.6–0.9 mm. broad; stem leaves usually ovate, commonly 6–9 cm. long and 2.5–5 cm. broad.

Calyx usually densely appressed hairy; lowest leaves well developed, usually cordate; cymes becoming loose in fruit; Kashmir to Nepal. . . . . *Hackelia uncinata* (Benth.) Fischer.

Calyx and especially the lobes, sparingly strigose or nearly glabrous; lowest leaves small, not cordate; cymes relatively few flowered and dense; Sikkim to Yunnan. *Hackelia brachytuba* (Diels) Johnson.

Mertensia Meyeriana Macbride, Contr. Gray Herb. **48**: 52 (1916); Popov, Fl. URSS. **19**: 249 (1953).

Mertensia Popovii Rubtz. Fl. URSS. **19**: 247 and 706 (1953).

The label associated with the type collection of *Mertensia Meyeriana* has the following data "On Chinese territory near Saisansk, so. Siberia, May 20, 1911, *F. N. Meyer* no. 727". When the species was published the geographic data were misread and were given incorrectly as "Zairansk, western Mongolia". A study of the itinerary of Meyer reveals that on May 20, 1911, he was near the Kazakh-Dzungaria boundary, southeast of Lake Zaisan, at about lat. 47° 30′ N and long. 85° 00′ E., probably at the west end of the Saur Mts. "Saisansk" is an old spelling for the town in East Kazakhstan appearing on recent maps as Zaisan or Zaysan. It is

clear, therefore, that the type of *M. Meyeriana* comes from the region designated in the Flora URSS as the "Dzungaro-Tarbagatai" floristic area, the very area in which *Mertensia Popovii* is endemic. The latter species is said to range, "In montibus Tarbagatai et Saur, satis frequens". Its lengthy description in the Fl. URSS applies perfectly to the type of *M. Meyeriana*.

Mertensia nemorosa (DC.), comb. nov.

Lithospermum ovalifolium Decne. in Jacquemont, Voy. Inde Bot. 121, t. 124 (1844). — In humidis nemorum ad Ouri [Uri on Jhelum River], May 4, 1831, *Jacquemont*.

Eritrichium nemorosum A. DC. Prodr. **10**: 123 (1846). — Based on *Lithospermum ovalifolium* Decne (1844), not *Eritrichium ovalifolium* DC. (1846).

A Kashmir plant most closely related to *M. racemosa* (Royle) Clarke of Kumaon, Bashahr and Kulu. It differs conspicuously in its blue-purple, rather than white corollas, and its coarser habit. Unlike *M. racemosa* its lower leaves are not subcordate at the base and the herbage usually darkens and becomes more or less chocolate-brown in drying.

The binomial *Mertensia ovalifolia* Brand, Pflanzenr. Heft **97**: 199 (1931), was coined by Brand and applied to two very different plants: *Eritrichium ovalifolium* DC. Prodr. **10**: 123 (1846), which is a species of *Trigonotis*, and *Eritichium nemorosum* DC. op. cit., our present species of *Mertensia*. In both applications Brand indicated that his binomial was a "nom. nov.". In Index Kewensis, Suppl. 9, *Mertensia ovalifolia* Brand is taken up as based upon *Eritichium ovalifolium* A.DC. This decision associates the name with the species of *Trigonotis* and makes it unavailable for our *Mertensia*.

The name "*Mertensia moltkioides*" has been applied to the present plant. Indeed, Coventry, Wild Fl. Kashmir **31**: 91, t. 46 (1930), has an excellent colored illustration of it under that name. *Mertensia moltkioides* Clarke, however, is based entirely upon the plant in Royle's Illustrations, which is described as *Myosotis moltkioides* (on pg. 305) but illustrated, on Plate 73, as *Anchusa moltkioides*. Royle's plant, from Pir Panjal Pass, must be reexamined. I believe it will be found to represent not the present species, but rather, *Mertensia primuloides* (Decne.) Clarke.

Mertensia exserta, nom. nov.

Craniosperm parviflorum Decne. in Jacquemont, Voy. Inde Bot. 126, t. 130 (1844). — Type from the northwest extension of the Pir Panjal Range, from the south side of the pass [i.e. Aliabad or Haji Pir pass] traversed by the road from Punch north to Uri on the Jhelum River, about long. 74° and lat. 34°, collected May 3, 1831 by Jacquemont. Not *Mertensia parviflora* G. Don (1837).

Moltkia parviflora (Decne.) Clarke, Fl. Brit. India **4**: 174 (1883).

Although it has elongate, much exserted stamens associated with a very reduced corolla, this plant otherwise agrees well with the species representing *Mertensia* in the western Himalayas. Authors, upon the basis of superficial resemblances, have classified this plant in the genera *Craniospermum* and *Moltkia*, but actually it has no immediate relationships with either genus. It is aberrant in *Mertensia* in having elongate, much exserted stamens associated with a reduced corolla, but in all other respects (and especially so in distribution, habit, fruit, and pollen) it shows definite relations with the Himalayan representatives of that genus. It obviously should be classified with the latter plants. I find it surprising that the species has not been transferred to *Mertensia* years ago.

Mertensia Trollii (Melch.) comb. nov.

Moltkia Trollii Melch. Notizbl. Bot. Gard. Berlin **15**: 115 (1940). — TYPE from Tragbal Pass, Kashmir, *C. Troll 7028*.

Mertensia Coventryana S. Clay, The Present-Day Rock Garden, pp. xx and 379, t. 27a (1937). — a provisional name for a cultivated plant; unaccompanied by technical description or Latin diagnosis. The published photograph, plate 27a, was made by B. O. Coventry at Banihal, Kashmir, 9000 ft. alt., May 17, 1929, and is to be associated with the herbarium-specimen, *Coventry 1448*, bearing the same data, which is now preserved at the British Museum.

This species is related to *Mertensia exserta* (= *Moltkia parviflora* Clarke) and confused with it in most herbaria. Both species have stamens conspicuously exserted from the corolla. *Mertensia Trollii* differs from its more common relative in having much larger corollas that have well developed lobes and five invaginate hemispheric appendages in the throat. The corolla lobes of M. Trollii are oblong or elliptic and 2–2.5 mm. long. Those of *M. exserta* are more or less triangular and usually 1–1.5 mm. long.

THE MECHANISM OF CONTROLLED GROWTH OF DWARF APPLE TREES *

A. G. Dickson and Edmund W. Samuels

Various methods have been used to dwarf apple trees and induce earlier fruiting. Standard varieties are budded or grafted on clonal varieties of dwarfing rootstocks. These dwarfing rootstocks have been used for at least several hundred years in Europe, and in recent years they have been introduced into North America. In this country dwarfing interstocks are often used. This method was described by John Rea in England in 1665 as follows: "I have found out another expedient to help them forward, that is by grafting the Cyen of the Paradise apple in a Crab, or other Apple-Stock, close to the ground, with one graft, and when that is grown to the bigness of a finger, graft thereon about eight inches higher, the fruit desired, which will stop the luxurious growth of the Tree, almost as well as if it had been immediately grafted on the forementioned layers, and will cause the Trees to bear sooner, more and better fruits" (Graves, 1950).

The practice of ringing the bark of fruit trees and vines to induce earlier fruiting is an even older art and was described by Virgil and Columella (Louden, 1850). In 1820 Williams described the effects of girdling grape vines as follows: "At the end of July and the beginning of August, I took annular excisions of bark from the trunks of several of my vines, and that the exposed alburnum might be again covered with new bark by the end of autumn, the removed circles were made rather less than a quarter of an inch in width. In every case in which circles of bark were removed, I invariably found that the fruit not only ripened earlier, but the berries were considerably larger than usual, and more highly flavored". The girdling of grape vines is still a standard practice (Weaver, 1955). The girdling of fruit trees, however, has been largely abandoned.

The practice of training the branches of fruit trees in a horizontal position to suppress growth and induce earlier fruiting has long been practiced in Europe. The knotting of the stems of trees by the Japanese to augment the production of miniature ornamental trees is also an ancient art.

A new technique for dwarfing trees has been developed recently, based upon the polarity of phloem or auxin transport (Sax, 1954). This practice involves the removal of a ring of bark from the trunk of a tree and replacing it in an inverted position. The inverted ring of bark is bound tightly with a rubber band until it is united with the wood. Because of the inverted polarity, the ring of bark acts as a phloem block, inhibiting the flow of plant nutrients to the roots of the tree.

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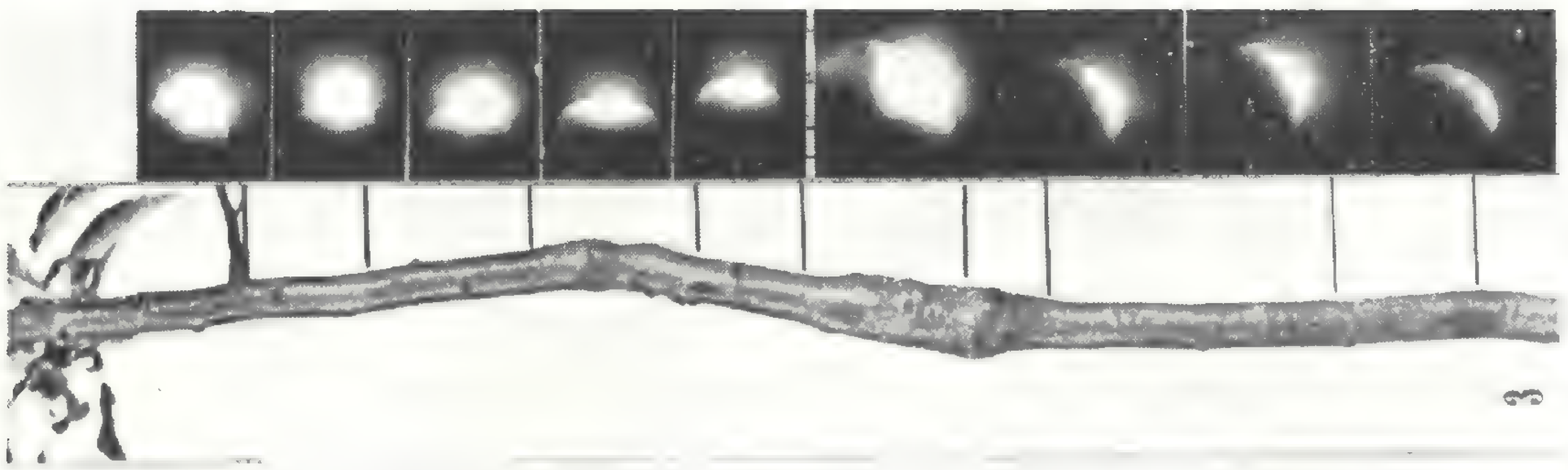
The physiological mechanism of the dwarfing effect of girdling, of dwarfing rootstocks and interstocks and of bending the branches of a tree was known by Thomas Andrew Knight nearly a hundred and fifty years ago. According to Knight (1822) the nutrient sap elaborated in the leaves passes down the bark, and when checked by girdling the bark, "the repulsion of the descending fluid therefore accounts . . . for the increased produce of blossoms, and the more rapid growth of the fruit upon the decorticated branch. . . ." The effect of the dwarfing rootstock was attributed by Knight (1822) to the obstruction of the descending sap at the graft union. He observed that "the effects produced, both upon the growth and produce of the tree, are similar to those which occur when the descent of sap is impeded by a ligature, or by the destruction of a circle of bark". In 1803 Knight, in discussing the fruiting of horizontal branches, observed that it was "by no means improbable, that the formation of blossoms may, in many instances, arise from the diminished action of the returning system in the horizontal or pendent branch". Thus, all of these mechanisms of dwarfing and induction of earlier fruiting are attributed to the checking of the flow of nutrient sap to the roots, which checks vegetative growth, and the accumulation of the nutrient sap in the top of the tree, which promotes flowering and fruiting.

The advent of radioactive tracers has made possible a more critical analysis of the physiological mechanism of dwarfing trees by bark inversion and dwarfing rootstocks and interstocks. In 1954 a series of experiments were started to trace phloem transport in dwarf apple trees with the aid of radioactive phosphorus.

The radioactive phosphorus was carried in a solution of KH_2PO_4 which had a radioactivity of about 1 mc. per ml. From 0.35 to 1.0 ml. of the solution was poured into a small glas tube which had been sealed at the lower end around the cut petiole of a leaf. One ml. of the solution was absorbed in from 35 to 45 minutes. Tests with a Geiger counter showed that the radioactive phosphorus reached the base of the tree, a distance of 1.5 to 2.0 feet, in from 4 to 6 hours, and that the accumulation of the isotope was well defined in about 3 days.

The first experiment was done on a Baldwin apple tree three years old which had been dwarfed by inverting two rings of bark the previous year. The isotope was fed through the petiole of a leaf on the lowest lateral branch. The speed of transport to the end of the lateral branch indicated that the isotope entered the xylem and passed up the stem in the transpiration stream. After its incorporation in the leaves into the organic nutrients it passed down the phloem. The distribution of the isotope three days after application is shown in figure 1. There was a gradual increase in radioactivity from the lateral branch down the trunk. The counts reached a maximum of 126,000 per minute in the inverted bark. Below the inverted rings of bark the count was greatly reduced to little more than 15,000 counts per minute. Obviously the downward flow of the isotope, and presumably of the organic nutrients was greatly retarded by the inverted rings of bark. As a result there was an accumulation of the isotope



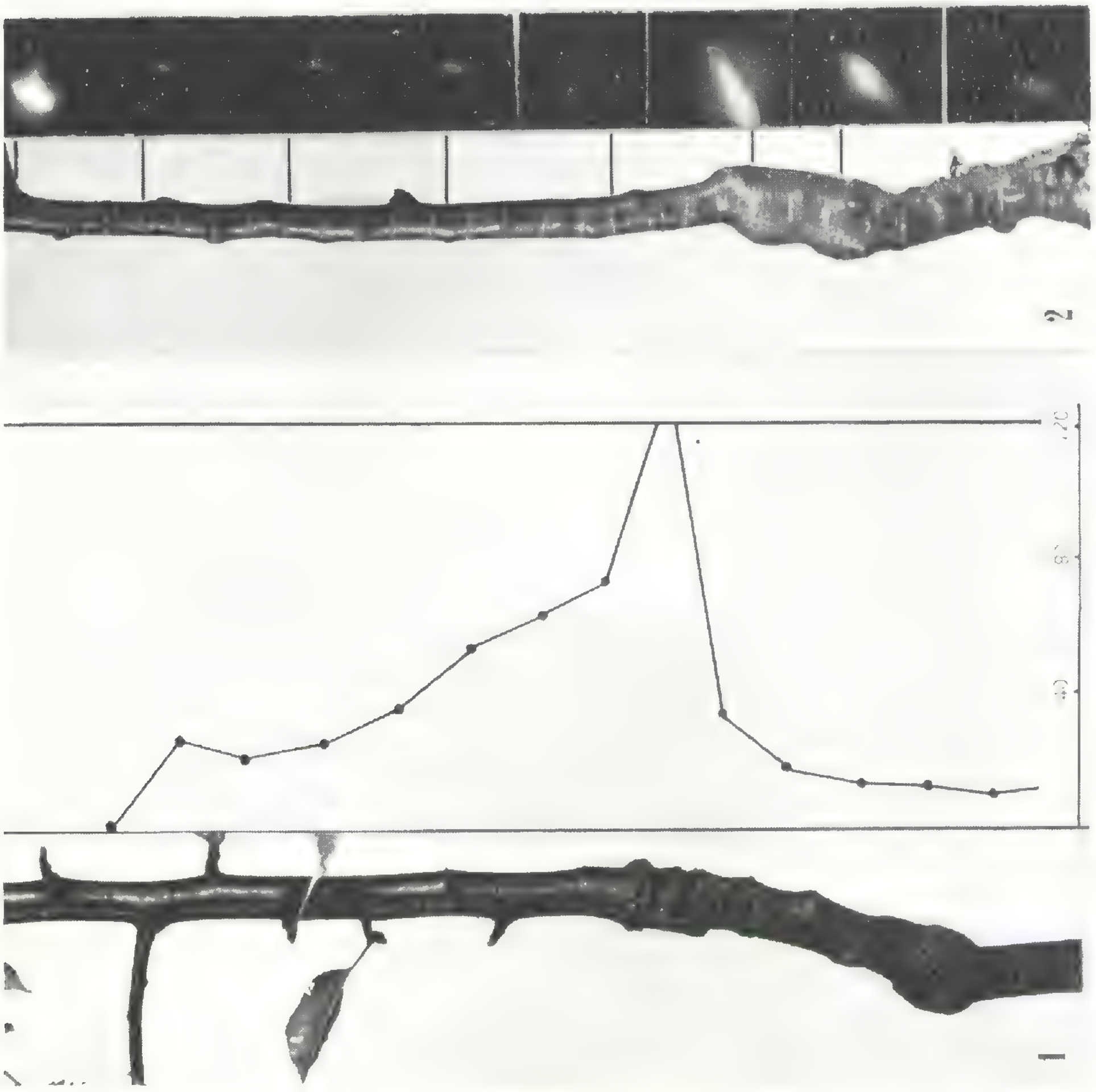


Fig. 1. The distribution of radioactive phosphorus in the trunk of an apple tree, which had been dwarfed by inverting two rings of bark, was measured with a Geiger counter three days after the application of the isotope. Note the great concentration of the isotope at the inverted ring of bark, and the great reduction in concentration below the bark inversion. In all cases the isotope was fed through a leaf petiole on the lowest lateral branch. (Measured in thousands of counts per minute.)

Fig. 2. The distribution of the isotope in the stem of an apple tree on a Malling IX interstock is shown by autoradiographs of transverse stem sections cut three days after the application of the isotope. Note the concentration of the isotope in the dwarfing interstock.

Fig. 3. The distribution of the isotope in the stem of an apple tree with a Clark's Dwarf interstock is shown by autoradiographs of stem sections cut seven days after the application of the isotope. The isotope is concentrated in the dwarfing interstock.

for a considerable distance above the bark inversions and phloem transport to the roots was reduced.

The tracing of the flow of the isotope down the trunks of young apple trees dwarfed by dwarfing interstocks presented a more difficult problem. The dwarfing interstocks have a relatively thick bark and the greater distance between the phloem and the outer surface of the bark reduces the beta radiation reaching the Geiger counter. In order to avoid the discrepancy caused by the differencse in thickness of the bark of the Malling IX and Clark's Dwarf interstocks and the rootstock and scion varieties, the concentration of the isotope was measured by autoradiographs of transverse sections of the trunk of the tree. The trunks of the young trees were cut in transverse sections about 5 mm. thick and numbered serially from top to bottom. Sections from various parts of the stem were mounted on a cellophane sheet and the cellophane was drawn tightly over a glass plate. Ansco isopan film, emulsion side down, was placed on the cellophane and the stem sections were exposed for 15–20 hours. All sections of a tree were exposed, developed and printed together to insure uniformity of treatment.

The isotope was fed into the end of a severed petiole of a five-year-old McIntosh apple tree which had been dwarfed by a Malling IX interstock on a *Malus sikkimensis* rootstock. Three days later, on June 14th, the trunk of the tree was cut into serial sections and autoradiographs of selected sections were made on June 16–17. There was a rather high concentration of the isotope at the junction of the lateral branch with the main trunk of the tree, but only very low concentrations in the lower trunk of the tree above and below the interstock. The Malling IX interstock, however, showed a great concentration of the isotope, as shown in figure 2.

In the third experiment the isotope was fed into a petiole on the lowest lateral branch of a three-year-old Starking apple tree on a Clark Dwarf interstock with a Virginia Crab rootstock. Stem sections were made seven days later and the autoradiographs were made with a 17 hour exposure. The results are shown in figure 3.

The high concentration of the isotope at the junction of the lateral branch with the trunk of the tree was again evident. Considerable radioactivity was found between the junction of the lateral branch and the Clark's Dwarf interstock, followed by a considerable increase in the interstock and a reduction below the interstock. Autoradiographs of four sections through the interstock were obtained and all showed a marked increase in radioactivity with the greatest concentration near the bottom of the interstock. It is evident that both Malling IX and Clark's Dwarf interstocks accumulate the isotope, and presumably the organic nutrients, carried down the phloem.

The fourth experiment was done with a four-year-old McIntosh tree which had been dwarfed by tying a knot in the *M. sargenti* interstock. In 1955 five such trees flowered and fruited heavily while the five adjacent control trees, in which the interstock was not knotted, bore no flowers. The isotope was applied in the usual manner and the stem sectioned three days

later. Autoradiographs showed a great concentration of the isotope at the junction of the lateral branch with the main stem, and a secondary and less marked concentration in the stem just above the knot and at the lower end of the knot before the stem began its upward turn. There was little radioactivity in the upper side of the loop or in the stem below the knot. Although the results were not as striking as those obtained with trees dwarfed by bark inversion or dwarfing interstock, there was some indication that the knot had restricted phloem transport.

The dwarfing effect of inverting a ring of bark appears to be caused by the checking of phloem transport, but the mechanism may involve other factors. Since phloem transport is not polar, the inversion of a ring of bark should not interfere with the pressure flow mechanism (Bonner and Galston, 1952). Auxin transport is, however, normally polar and its basipetal movement would be prevented by inverting a ring of bark. Inhibition of auxin flow is indicated by the fact that the dormant buds below the inversion are stimulated into active growth and new growth continues during the summer even when the first sucker branches are removed. Some release of dormancy is effected by simply removing a ring of bark and replacing it in the normal position, but this effect is much more temporary.

The deficiency of auxin in the inverted bark may inhibit phloem transport directly, or indirectly, by the inhibition of cambial activity and growth of the stem. It is known that the inversion of a ring of bark suppresses the growth of the stem in the inverted region, and in a rapidly growing tree there is a great overgrowth of the stem above the inversion.

The dwarfing effect of the dwarfing interstocks also appears to be associated with the retardation of phloem transport. Since the dwarfing interstocks are normally polarized there should be no blocking of the basipetal movement of the auxin. In contrast to the inverted ring of bark the dwarfing interstock grows more rapidly than either the stem of the rootstock or the stem of the scion variety. Perhaps both phloem and auxin transport is retarded in the dwarfing interstock. It may be of some significance that the most effective dwarfing interstocks are varieties which are natural dwarfs when grown on their own roots.

The dwarfing effects of girdling the bark, the use of dwarfing rootstocks and interstocks and the inversion of a ring of bark on the trunk of the tree appear to be associated with the retardation of phloem transport, but dwarfing effects may also be caused by other factors. Peach trees dwarfed by budding them on *Prunus tomentosa* rootstocks show no retardation of the isotope at or below the graft union, nor is there any overgrowth of the dwarfing rootstock as is found with dwarfing Malling apple rootstocks. Even in certain graft combinations of apple varieties the dwarfing effect is not due entirely to the graft union or to the stem of the rootstock (Sax, 1954).

The organic nutrients accumulated at, or above, the phloem block may diffuse into the xylem and be carried by the transpiration stream to the branches where they are used in the production of fruit, as was suggested by Knight in 1820. There is amply experimental evidence to show that

nutrient may pass from phloem to xylem or from xylem to phloem (Crafts. 1951). Colwell (1942) found that radioactive phosphorus applied to the leaf will move down the stem to, but not beyond, a deleted ring of bark, and that immediately above the ring the isotope is found in the xylem as well as the phloem. Greene (1937) obtained a higher starch and sugar content of spurs on ringed branches of Grimes Golden apples than was found on the control branches. Leonard (1938) found that the leaves of an apple variety grown on a Malling IX dwarfing rootstock had a higher content of soluble carbohydrates than those of the same variety of apple grown on a standard rootstock. Stanley Burg in 1954 (unpublished data) found that within a week after the inversion of a ring of bark on the trunk of a maple tree the carbohydrate content of the leaves was greatly increased. Thus the phloem blocks not only check the flow of organic nutrients to the roots, but also increase the organic nutrients of the leaves.

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SUMMARY

Apple trees may be dwarfed and induced to fruit earlier by grafting them on a dwarfing rootstock or interstock, or by inverting a ring of bark on the trunk of the tree. The mechanism of these dwarfing effects was

studied with the aid of radioactive tracers. Radioactive tracers were fed through the petioles of the leaves of the lateral branches of young trees. Several days later the distribution of the isotope in the trunk of the tree was determined with a Geiger counter and by autoradiographs of transverse stem sections. The great concentration of the isotope in the dwarfing interstock or in the inverted ring of bark indicates that the dwarfing effect may be caused by checking the flow of organic nutrients to the roots, but the mechanisms involved may be indirect and diverse.

A RUST ON WOODWARDIA FIMBRIATA

J. H. FAULL

THREE RUSTS have been described on chain ferns; a fourth is recorded as having a chain fern added to its list of hosts. They are: *Uredinopsis Arthurii* Faull II [1], II [2], III on *Woodwardia virginica* (L.) Sm.; *U. Arthurii* var. *maculata* Faull II [1], II [2], III on *W. areolata* (L.) Moore; *Milesia Tobinagai* (Hirat.) Faull II on *W. japonica* Sm. (described as *Milesina Tobinagai* by Hiratsuka in Journ. Jap. Bot. 12: 271, 1936); and *Hyalopsora Polypodii* (Pers.) Magnus on *W. orientalis* Sw. *Uredinopsis Arthurii* is reported from the eastern part of North America and not elsewhere; it is recorded from Alabama to Quebec and from Bermuda to Indiana and Michigan. *Uredinopsis Arthurii* var. *maculata* is likewise known to occur in the eastern part of North America only, but in a much narrower range; it is recorded from Alabama to Maine. *Milesia Tobinagai* is from Japan; it was recorded and described from material collected on the island of Kiushû. *Hyalopsora Polypodii* on *W. orientalis* is reported from Japan; it, too, was recorded from the island of Kiushû. Besides these four there is also an unreported species; that one is on *W. fimbriata* Sm. in California. It is recorded and described below.

Before doing so, however, I should say that I have been reluctant to describe it as a new species. That is so because the urediospores (the only spores so far observed) are like those of *Milesia polypodophila* (Bell) Faull as to size, form, and the not uncommon habit of branching at or near their apices. Of course this rust may be *M. polypodophila;* but many facts have yet to be determined before the answer can be given. Thus: *M. polypodophila* has been reported from eastern North America only; as for its fern hosts there it has been reported only on *Polypodium virginianum;* its alternate host is a conifer, but the loose-broom effect on it is unique; besides that, spermogonia and peridermia are not produced until three years after its infection; it is the only known *Milesia* characterized by such a phenomenon; moreover, its spermogonia are distinctive as to size, length of period of development, abundance of spermatia and length of period of spermatial discharge. So, I have deemed it best to regard this rust on *W. fimbriata* a distinct species pending determination of all its essential features.

Milesia acuta Faull, sp. nov., II.

Spermogonia et aecia ignota. Uredia hypophylla, epidermide tecta, pustulata, rotundata, 0.15–0.5 mm. diam., peridio ex cellulis hyalinis composito cincta; urediosporae fusiformi-obovatae vel fusiformes, acutae

vel acuminatae, subsessiles, hyalinae, 12–19 × 32–62 μ, plus minusve circa 16 × 51 μ; paries sporae hyalinus, levis, tenuis. Telia ignota.

Hab. in foliis *Woodwardiae fimbriatae* in California.

O and I. Spermogonia and aecia unknown.

II. Uredia hypophyllous, subepidermal, on discolored areas of indefinite extent, pustular, round, 0.15–0.5 mm. in diameter; peridium hemispheric, peridial cells isodiametrically to irregularly polygonal, 5–11 × 5–14 μ, with walls about 1 μ thick; urediospores hyaline, abundant, extruded in tendrils or masses, very short-stalked, fusiform-obovate or fusiform, acute or acuminate at the apex, occasionally forked or branched at or near the apex, narrowed below, 12–19 × 32–62 μ, averaging about 16 × 51 μ, wall of spore thin, about 1 μ thick, smooth, with 4 to 6 germ pores in pairs towards poles or at equator.

III. Telia unknown.

HOSTS AND DISTRIBUTION:
O and I. Unknown.
II. *Woodwardia fimbriata* Sm., in California.
III. Unknown.
TYPE LOCALITY: Mt. Tamalpais, Marin County, California. II.
ILLUSTRATIONS: Text-figure 1.
SPECIMENS EXAMINED. —
CALIFORNIA: Mt. Tamalpais, Marin Co., March 31, 1926, *H. E. Parks*; TYPE. — Mt. Tamalpais, May 30, 1935, *L. Bonar*. — Big Sur, Monterey Co., August 14, 1937, *L. Bonar*. — Darlingtonia, Del Norte Co., Feb. 22, 1942, *H. E. Parks*.

The materials studied were all sent by Professor Lee Bonar; too, the specimens of the last lot were sent at the request of Mr. H. E. Parks. Included with this last lot were three microscopic slides of microtome sections made from a part of the collection. They show that the stoma of a uredium is directly under a leaf stoma; also that the opening is encircled by sharp-pointed peridial cells.

On some of the packets there is written "*Hyalopsora Woodwardiae* Jackson, n. sp." This is a ***nomen nudum et ineditum***.

Examination of an abundance of urediospores from the type of *Milesia Tobinagai* shows that they are stout and that they are rounded at their apices. They measure 12–19 × 19–35 μ, and they average about 17 × 25 μ. A good description is given by Hiratsuka in his "A Monograph of the Pucciniastreae", p. 157–8, 1936. There is no likelihood of confusion between *M. Tobinagai* and *M. acuta*.

Woodwardia fimbriata, the one recognized host of *Milesia acuta*, extends northward from California into British Columbia. It has passed under the names *W. radicans*, *W. spinulosa* and *W. Chamissoi*. What the coniferous generic host is and what the comparative effects on its species are, remain for experimentation.

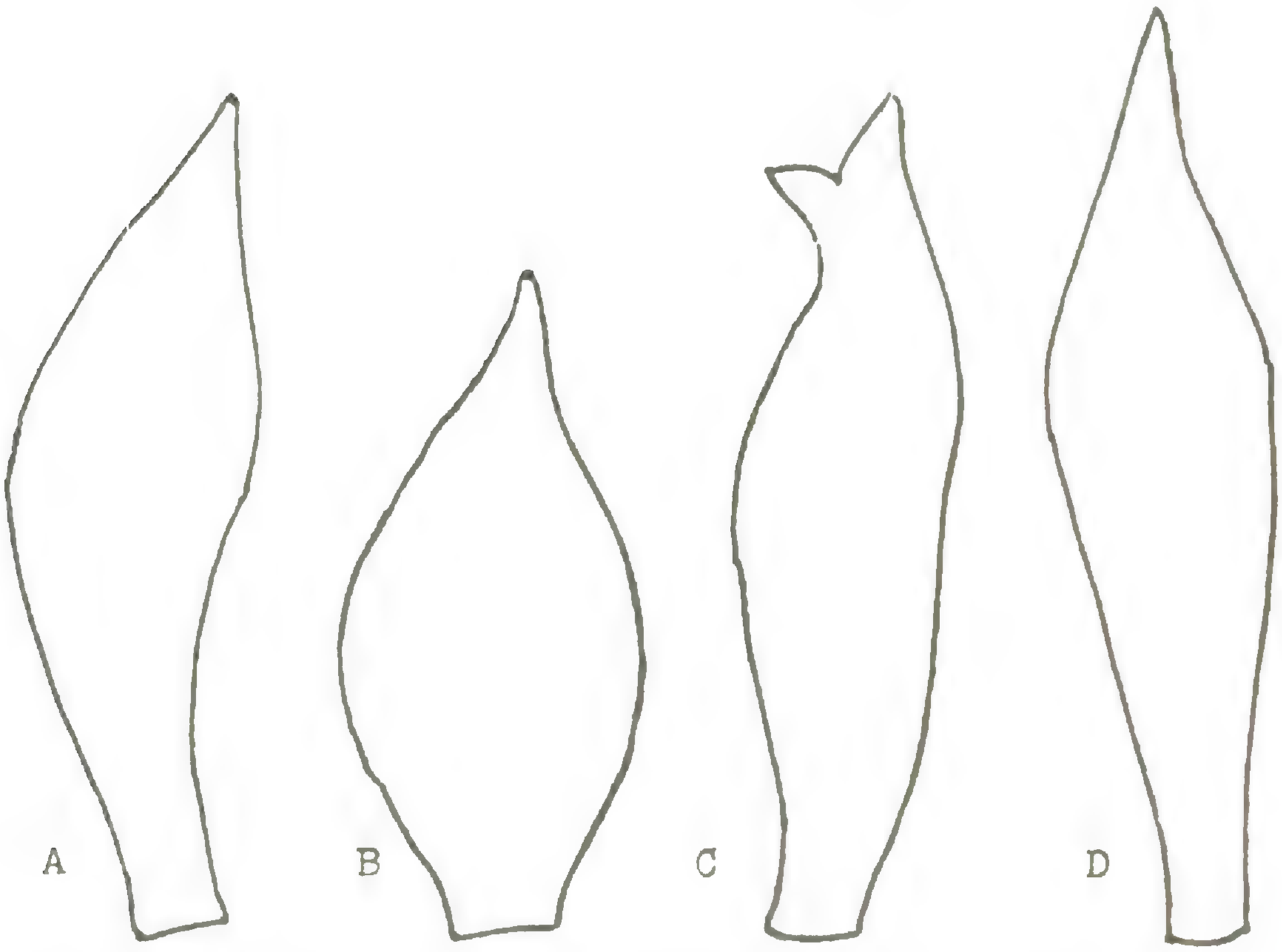

FIG. 1. *Milesia acuta*, sp. nov. Outlines of four urediospores from same microscopic mount. The one at the extreme left is about average size — 16 × 51 μ.

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STUDIES OF THE GENUS COCCOLOBA, II. THE IDENTIFICATION OF COCCOLOBA SWARTZII MEISNER AND COCCOLOBA BARBADENSIS JACQUIN AND THEIR RELATIVES

RICHARD A. HOWARD

IN A STUDY of the genus *Coccoloba* in Cuba published in 1949 (Jour. Arnold Arb. 30: 388–424), I recognized *Coccoloba swartzii* Meisner as a species of *Coccoloba* of wide distribution in the West Indies. A complete understanding of this species and a discussion of its variations and distribution was not possible at that time, despite the fact I was re-establishing a species not recognized for nearly fifty years. In 1950 I made an extensive trip through the Greater and Lesser Antilles to study the distribution and variation of species of *Coccoloba* in the field. In succeeding years I have had the opportunity of field study in the Bahamas and Jamaica. A number of trips to Jamaica to study the plants growing on bauxite soils has permitted the examination of many populations of *Coccoloba swartzii* which is based on material collected in Jamaica. The problems presented by this polymorphic species and its insular variations are not all solved but I hope that this paper will remove some of the confusion currently present in the identification and description of these plants in the West Indies.

I am indebted to the American Philosophical Society for a grant from the Penrose Fund in 1950 which initiated the original field study of the genus *Coccoloba*, to the Institute of Jamaica and, indirectly, to the Reynolds Jamaica Mines and the Kaiser Bauxite Company for additional financial support which made possible subsequent observations of *Coccoloba* while engaged in a field survey of plants on bauxite soils. During the summer of 1955 I visited many herbaria and botanical gardens in Europe and acknowledge with pleasure the permission granted me by the directors and curators of the following herbaria to study critical and related materials in the following institutions: Botanischer Garten und Museum, Berlin-Dahlem; Botanische Staatssammlung, München; British Museum, London; Conservatoire et Jardin botaniques, Genève; Linnean Society of London; Naturhistoriska Riksmuseum, Stockholm; Royal Botanic Garden, Edinburgh and Royal Botanic Garden, Kew. Additional herbarium ma-

terials have been borrowed from many institutions in the United States. I am particularly appreciative of the patience of the directors and curators during the long period that specimens have been on loan from the Gray Herbarium, the Field Museum, the New York Botanical Garden, the University of Michigan and the Missouri Botanical Garden.

Coccoloba swartzii Meisner is the name which must be applied to the common species of the West Indies previously called *C. barbadensis* by Lindau, *C. diversifolia* by Lindau, Fawcett & Rendle and Britton, *C. coronata* by Millspaugh and *C. punctata* by Krebs, Eggers and Northrop. *Coccoloba borinquensis* Britton and *C. urbaniana* are now recognized as one form of this species, while *C. neglecta* Fawcett & Rendle is included within the species concept. As the name *C. diversifolia* Jacq., the name most widely used, must be substituted (Jour. Arnold Arb. 30: 421–424. 1949) for *C. laurifolia* (of all recent floras), a considerable readjustment of nomenclature is necessary in terms of the usage found in the present-day floras of the West Indies.

The name *Coccoloba barbadensis* Jacq. is the oldest name commonly applied to this species in floras in general use. This species was originally described very briefly by Jacquin in his Enumeratio 37. 1760. It listed in synonymy "Guajabasa foliis oblongis" from Houston's catalogue. An illustration of the species was supplied in Jacquin's second report of the species in his Observationum Botanicarum 1: 18, *pl. 8.* 1764; however, the description was not amplified. A specific location for the origin of this plant was not given in either description and this has caused a great deal of the confusion regarding the application of this name. The assumption has been made that Jacquin would have applied the specific name "barbadensis" to a plant from the West Indies, presumably the island of Barbados, and all recent monographers have attempted without success to associate Jacquin's species with specimens from Barbados or one of the islands near Barbados in the Lesser Antilles. In an attempt to identify accurately both Jacquin's plant and its origin, I learned of the earlier similar considerations by Messrs. Sandwith and Dandy and both have been most generous of their time and effort in assisting me. Mr. Dandy has supplied copies of his correspondence on this problem and secured for me photographs of the Jacquin material in the British Museum. However, these observations still did not resolve the problem in my mind and it was clarified only after a visit to the British Museum and personal study of the authentic material. The herbarium of the British Museum contains two sheets referable to Jacquin's herbarium. The original Jacquin sheet, to be considered the type of the species, is the one illustrated in Observationum Botanicarum. The illustration is accurate and the specimen drawn is sterile, being the terminal portion of a shoot, not necessarily an adventitious shoot. Jacquin had only sterile material at the time of publication for he mentions "racemus vero sive floriger sive fructiger desideratur omnis." Although Jacquin was in the West Indies, there is no indication that he collected the material himself. His itinerary included Martinique, St. Vincent, Grenada, Guadaloupe, St. Kitts, St. Eustatius, St. Martin,

St. Barts, Haiti, Jamaica and Cuba, as well as Venezuela and Colombia in South America and the islands of Curacao and Aruba. The known material of *Coccoloba* from these areas does not match the sterile specimen illustrated by Jacquin.

In the herbarium of the British Museum is a second sheet from the Miller Herbarium called *Coccoloba barbadensis* Jacquin which was collected by Houston. Mr. Dandy had written that this specimen possessed an old inflorescence axis without flowers or fruit and that "it is exactly the same as Jacquin's *C. barbadensis* and may possibly represent the same gathering." While this could not be identified by the photograph, personal observation last summer satisfied me that Mr. Dandy was correct in concluding that they are identical. I later discovered still a third sheet referable to Jacquin's species in the herbarium at Cambridge. This also was a Houston collection and also possessed an old inflorescence axis. If the sterile material which Jacquin described came from the Houston collection, as seems apparent, an accurate determination of this species seems possible. Houston visited Cuba and Jamaica, but more important, he visited Mexico and Campeche (Yucatan) in particular. It is among Mexican collections that the type material of *C. barbadensis* Jacquin can be matched with certainty and it is to Mexican collections that the name should be applied.

To Meisner must go the dubious credit of creating all the confusion, for the reference in DC. Prodr. **14**: 153. 1856–7 is apparently the earliest reference of the Jacquin species to the island of Barbados. Meisner, however, saw only a sterile fragment in the Berlin herbarium which appears to be an Ehrenberg collection from St. Thomas. At the same time, Meisner described a new variety, *C. barbadensis* var. *mexicana*, based on a collection by *Schiede 1151* from Mexico. Lindau (Engl. Bot. Jahrb. 13: 187. 1890) raised this variety to a species (*C. schiedeana*), referring to it several additional collections. It is among the many collections now called *C. schiedeana* that one finds exact matches of the type material of *C. barbadensis*. *Coccoloba schiedeana* must be considered a synonym of *C. barbadensis* Jacq. and several species more recently described will also be assigned here in a later paper.

Additional support for considering *Coccoloba barbadensis* a species not of Barbados but of Mexico, particularly the Yucatan area, can be found in two companion cases. In Observationum Botanicarum, Jacquin described a second sterile species of *Coccoloba*, *C. emarginata*, which is also illustrated. This is now known as *Neomillspaughia emarginata* (Gross) Blake. Although the name is based on *Podopterus emarginatus* Gross, the species are the same. A second case is the species *Paullinia barbadensis* Jacq. of the Sapindaceae. Radlkofer (Pflanzenreich IV 165: 334. 1931) recognizes this Jacquin species as occurring only outside of Barbados, although it has the same specific name *barbadensis*. Finally, the assignment of *C. barbadensis* to Mexico is supported by applying proper emphasis to Jacquin's citation of a reference to Houston's catalogue in the original description.

In his monograph of the genus *Coccoloba* (Engl. Bot. Jahrb. 13: 148. 1890), Lindau recognized *C. barbadensis* Jacq. (Enum. 37. 1760 and Observ. 1, 18, *t. 8*) and listed in synonymy with it *C. diversifolia* Jacq. (Hist. Stirp. Am. p. 114, *tab. 76.* 1763 & Pict. *tab. 113.* 1780). However, in a treatment published in Urban's Symbolae Antillanae (1: 223. 1899) he cited new references and reversed his treatment of these two names, accepting *C. diversifolia* Jacq. (Enum. 19. 1760) and placing in synonymy *C. barbadensis* (Enum. 37. 1760), apparently on the basis of page priority. In this treatment he has been followed by Britton and his co-authors in treatments of the genus, for The Bahama Flora and the Flora of Puerto Rico and the Virgin Islands, as well as Fawcett & Rendle in the Flora of Jamaica. As *C. barbadensis* must now be used for a Yucatan species and as *C. diversifolia* Jacq. must be applied to the West Indian species with pedicelled fruit generally called *C. laurifolia* (Jour. Arnold Arb. 30: 423. 1949), it should be clear, therefore, that *C. barbadensis* Jacq. and *C. diversifolia* Jacq. are not identical and the synonymy used in current floras is incorrect. Further, as neither name can apply to the West Indian common species under consideration, a new name must be found.

The names *Coccoloba punctata* and *C. coronata* which some authors have used for this species are not available, as both are referable to *C. venosa* L. (Syst. Nat. ed. 10, 1007. 1759). *Coccoloba punctata* L. was published in the second edition of the Species Plantarum, page 523. 1762 and *C. coronata* Jacq. (Hist. Am. Stirp. 114, *tab. 77*) is based on an erroneous Plukenet illustration, the fruits of which are not *Coccoloba* and the leaves represent the validly published *C. venosa* L.

The next available name is *Coccoloba swartzii* Meisner (DC. Prodr. 14: 159. 1856–7) which was based on specimens in the DeCandolle herbarium at Geneva collected by Swartz, West and Forsyth. The description given applies primarily to the Swartz material and it is apparent that Meisner considered this the type specimen, although there is no published indication of such a decision. The Meisner personal herbarium is at the New York Botanical Garden and a fragment of the Swartz specimen from the DeCandolle herbarium was selected as representative of the species. Although none of the specimens cited by Meisner is given a specific island reference, it is probable that the Swartz material was from Jamaica, the "Forsyth" material (in reality that of Dr. Wright) also from Jamaica and the West material from St. Croix. Specimens in the collections at Stockholm, Berlin and Copenhagen match those cited by Meisner and carry more complete information. Modern collections which match the Swartz type of this species are all from Jamaica; e.g. *Harris 5500, 8062, 11639*; *Britton 430, 919, 3236, 3757* and *Howard 12022, 12031.* Fawcett and Rendle cite some of the specimens recently mentioned in their treatment of the genus *Coccoloba* for the Flora of Jamaica. However, they overlooked the species described by Meisner and call the material *C. diversifolia* which is here referred to *C. swartzii.* Lindau recognized *C. swartzii* of Meisner but distinguishes this from his *C. barbadensis* by the absence of pubescence on the rachis.

I am referring to *Coccoloba swartzii* material from St. Lucia and other islands to the north in the Lesser Antilles, as well as collections from the Leeward Islands, the Virgin Islands, Puerto Rico, a few specimen from Hispaniola and Cuba and material from Jamaica and the Bahamas. I have studied living plants in each of the areas designated and have examined over 150 different collections as herbarium specimens. On the basis of comprehensive field studies, to develop the background for interpretation of the older herbarium specimens, I have concluded that *Coccoloba swartzii* is a polymorphic species with considerable morphological variation present in individual plants, populations and geographic areas. The type material of the species can be considered as one end of a line within the species and is not typical nor characteristic of the species from the consideration of its geographical entirety. As is usual in *Coccoloba*, the plants are functionally unisexual and in *C. swartzii* in particular the difference in aspect between the functionally staminate plants with clustered flowers and the functionally pistillate plants with generally single flowers is striking and has been valued much too highly in establishing species characteristics. The morphological variation present in *C. swartzii* in the development of adventitious shoots both following injury and without injury is also striking. A tree of this species on the island of Nevis, in a protected and cherished bit of woodland, was about the largest tree on the island. This specimen was fully eighty feet tall and had a diameter of three feet at breast height. The first branch was fifty feet above the ground and nearly a foot in diameter at the trunk. Twenty feet from the main trunk there arose from this horizontal branch an erect shoot with the larger leaves, long internodes and ochrea typical of adventitious shoots. The leaves were three or four times the size of the leaves on all the other branches and parts of this plant. There was no apparent injury responsible for the development of this shoot which, if taken alone, would have represented material clearly distinct from the main tree.

Another tree in a river valley near Casa Pilota on Martinique (*R. A. & E. S. Howard 11712*) possessed adventitious shoots which bore leaves 70 cm. long and 25 cm. broad. These were the largest adventitious leaves on one of several trees in the area which had been partially cut for firewood. The tree in question had branches with round leaves averaging 10 × 8 cm. and from the base of one of these branches the adventitious shoots with the larger leaves were developed below the scar of a machete cut. Without field knowledge of these plants, the proper interpretation of many of the specimens in herbaria has been faulty.

The variation in leaf size and shape, even without the effects of trauma, are sufficient to create difficulty for the herbarium taxonomist. Additional variations are possible in thickness, texture and aspect of the leaves when dry. An example of this is *C. neglecta*, described by Fawcett & Rendle in the Journal of Botany (**51**: 124. 1913). *Harris 5094* was cited as the only specimen. Shortly after the paper appeared, Urban apparently suggested the Harris number was a mixed collection, for in the herbarium at Berlin is a letter from Fawcett to Urban acknowledging that the leaf of *Harris 5094*

which Urban had sent was actually *C. diversifolia* (e.g. *C. swartzii*). Thus in their later treatment of *C. neglecta* for the Flora of Jamaica, Fawcett & Rendle cited "Harris 5094 in part" and also *Harris 5233*. I have seen five sheets of the type number and three sheets of *Harris 5233*. I can only conclude that the *Harris 5094* is not a mixed collection as Urban and Fawcett & Rendle supposed, but only variations to be expected within one collection, even from a single tree of this species. Fawcett & Rendle distinguish *C. neglecta* from *C. swartzii* by the fact that the former has inconspicuous veins and the latter more conspicuous veins in the leaves, in dried condition. This character reflects only the variation in thickness of the leaves. The character of pubescence altered in successive published descriptions of this species is likewise a variable character and is not supported in the specimens I have seen or those cited by the authors. *Coccoloba neglecta*, here reduced to the synonymy of *C. swartzii*, is another example of the variations present in this species which become exaggerated in isolated herbarium specimens.

The variations in leaf shape are particularly evident in the aspect of the leaf base. Plants from Jamaica, the Bahamas, Hispaniola and Puerto Rico tend to have an oblique cordate leaf base. Those from the Lesser Antilles tend to be cuneate at the base. Specimens from Jamaica, Hispaniola and Puerto Rico tend to dry a characteristic dull black color, while those from the Virgin Islands become bright yellow-green and glossy when dry; those from the Lesser Antilles are neither black nor glossy but dull grayish green. The collections from the Bahamas and the Virgin Islands have consistently smaller leaves. Specimens which I collected in South Bimini of the Bahamas have leaves as small as 2 cm. long and 1 cm. wide grading on the same plant and in the same population to plants with leaves comparable to those of plants from Jamaica. The length of the inflorescence varies with the size of the leaf. Lindau has annotated many of the herbarium collections cited from the Bahamas with an unpublished variety name referring to the small leaves.

There is substantial variation also in the size and some variation in the shape of the fruit. So few specimens are represented by fruit, however, that it is impossible to evaluate the associated characters. In general, the fruits are larger in specimens coming from the Virgin Islands and the Lesser Antilles than they are from the northern and western ends of the range.

I have recognized two forms of this species, forma *pubescens* and forma *urbaniana*. Each is recognized for a different reason. *Coccoloba swartzii* forma *pubescens* is discussed in more detail later in this paper. This taxon includes plants retaining pubescence into maturity and specimens have been assigned here from Cuba, Guadeloupe, Barbuda and Antigua.

Where possible in the field, I have studied germinating seedlings of all species. Seedlings of *C. swartzii* were most abundant in St. Lucia where, under a thirty-foot tree on a dry hillside between Le Toc and Cul de Sac Bay, I discovered the ground littered with old and new fruits, with a fair percentage already germinated. A specimen was made of the parent tree

(*R. A. & E. S. Howard 11377*) and the young seedlings. The cotyledons were still contained within the fibrous fruit coat and vascular remains of the hypanthium. A tap root was well developed. The hypocotyl, petioles of the cotyledons and the apical bud were densely long-pubescent, literally pilose-pubescent. A few older seedlings in the vicinity showed evidence of short hairs, but none of the mature plants revealed a persistent pubescence. Germinating seedlings located beneath plants of *C. swartzii* forma *pubescens* on Antigua are almost identical in the pubescent characteristics. However, in the parent plants of these seedlings the pubescence had persisted. These pubescent plants are recognized as forms because of a scattered occurrence, yet present in sufficient, although localized, numbers to be significant populations.

The second form recognized consists of conspicuous anomalous, perhaps teratological, plants known from restricted areas in Puerto Rico. This taxon is also discussed in more detail later in this paper, but the entity is recognized as a form because its conspicuous character, coupled with its restricted geographical distribution, would suggest evaluation as a geographical variety if the numerous intermediate forms were not known. As the intermediate forms do have a validly published name which cannot be applied to an anomalous condition, it seems desirable to use nomenclature here to indicate the variation recognized within the species.

The variation recognized in *Coccoloba swartzii* is greater than that found in other species of the genus in the same area. *Coccoloba uvifera*, *C. diversifolia*, *C. pubescens* and *C. krugii*, which have comparable ranges, have far greater morphological uniformity. It had been hoped that cytology might offer further light on the nature of the variation seen and to that end extensive collections of fruits and seeds were made and have been received since. However, less than one percent of the fruits proved viable and only two plants were grown past the cotyledon seedling stage from eighty different lots of fruits. Root tip chromosome counts have not been obtained from these, despite numerous attempts.

I strongly suspect that some apomictic methods of reproduction will be found in the genus *Coccoloba* and probably in *Coccoloba swartzii*. The numerous small variations which seem characteristically representative of insular floras in this species are not at present large enough to be taxonomically significant, but are potentially of species magnitude. It is significant also that even the oldest plant distribution records of the species and its variations based on herbarium specimens can be verified today. This is remarkable when one considers the severe population pressures in the West Indian Islands, the effects of hurricanes and the passage of time. In other words, the variations within the species have not been chance collections of botanists in the past, but are definite populations which are being perpetuated. Such small variations, when represented by isolated collections and handled by taxonomists who emphasize minute characters, result in the taxonomic creation of "difficult" genera. *Coccoloba* is indeed such a genus, with relatively few good morphological characters and extremely large variations often involving the same characters.

Other species which could be considered closely related taxonomically to *C. swartzii* are *C. pyrifolia*, *C. microstachya* and *C. krugii*. These are described and discussed for comparison, since material of *C. swartzii* has been incorrectly associated with these species by many botanists and authors.

Coccoloba swartzii Meisner, DC. Prodr. **14**: 159. 1856; Lindau, Engler Bot. Jahrb. **13**: 157. 1890; Howard, Jour. Arnold Arb. **30**: 420. 1949.

Coccoloba swartzii var. (?) *portoricensis* Meisn. DC. Prodr. **14**: 160. 1856; Lindau, Engler Bot. Jahrb. **13**: 157. 1890; Britton & Wilson, Sci. Surv. P.R. **5**: 270. 1924.

Coccoloba barbadensis Lindau, Engler Bot. Jahrb. **13**: 148. 1890, not Jacq.

Coccoloba diversifolia Lindau, Symb. Antill. **1**: 223. 1899 and most recent authors, not Jacq. (Howard, Jour. Arnold Arb. **30**: 421. 1949.)

Uvifera swartzii Ktze., Rev. Gen. **2**: 562. 1891.

Coccoloba neglecta Fawcett & Rendle, Jour. Bot. **51**: 124. 1913; Flora Jam. **3**: 116. 1914.

Coccoloba punctata Grisebach, Krebs, Eggers, and Northrop, not Linnaeus.

Coccoloba coronata of Millspaugh, not Linnaeus.

Trees 8–20 m. tall; branches terete, the youngest puberulent, becoming glabrate, the nodes slightly tumid; ochrea 10–12 mm. long, the basal portion 3–5 mm. long, coriaceous, persistent, the upper portion 5–7 mm. long, membranaceous, deciduous, puberulent to glabrate; petioles attached at the base of the ochrea, 10–18 mm. long, puberulent or glabrate; leaf blades ovate to elliptic, 2.2 × 1.3, 7 × 5, 11 × 9, 15 × 7.5 cm. long and broad, entire, coriaceous, usually turning black on drying, glabrous, pit-like depressions on the upper surface, small glands on the lower surface, the midrib and veins inconspicuous or flat above, prominent below, the primary veins 6–7 pairs, arcuate anastomosing, secondary venation conspicuous, reticulate, the apex acute, often rounded, the base narrowed, rounded or slightly cordate, usually oblique; leaves of adventitious shoots on petioles 1.5–2.5 cm. long, the blades generally ovate to lanceolate, 23 × 8.5, 45 × 18.5 to 70 × 25 cm. long and broad, the apex acute to acuminate, the base rounded; inflorescence terminal, 10–15 cm. long, the rachis glabrous or with glandular exudate, rarely papillose; staminate flowers in clusters of 3–5 flowers with tightly concentric membranaceous ochreolae forming a truncate cylinder after the flowers have fallen; pistillate flowers solitary, the ochreolae erect in flowers, flattened against the rachis in fruit, the bracts ovate, 1–1.5 mm. long, the ochreolae membranaceous 1–1.5 mm. long, the flowering pedicels shorter than the ochreolate, the hypanthium 0.5 mm. long, the perianth lobes 1–1.5 mm. long, the fertile stamens with filaments 1 mm. long; fruit ovoid 8–10 mm. long, 6 mm. in diameter, the perianth lobes 1–1.5 mm. long coronate in fruit.

HOLOTYPE: Swartz s.n. DeCandolle Herbarium, Geneva.

LOCAL NAMES: Redwood (Leeward Islands), saltwood (St. Lucia), boarwood (Jamaica), wild grape, red grape, boarwood (Jamaica), tie tongue, bastard pigeon plum (Bahamas).

ECONOMIC USES: *Coccoloba swartzii* is widely used in the Lesser Antilles and the Virgin Islands as a source of wood for charcoal. In many cases every plant on a hillside had been cut at least once and the adventitious shoots which were developing were carefully pruned and protected for the same eventual purpose. Duss reports the wood to be excellent for construction purposes, but such usage in the French Islands has not persisted.

Jamaica: CLARENDON: Savoy, *Harris 11639* (C, F, GH, NY, MO, US); Peckham Woods, *Harris 11194* (NY, US); Croft's Mts., *Harris 11219* (F, NY, US). MANCHESTER: New Green, *Britton 3757* (NY); Mandeville, *Britton 3732* (NY), *3236* (NY). PORTLAND: Green Ridge, *Eggers 3732* (C); Claverty Cottage, *Harris 5088* (C, US); Mt. Pleasant, Stony Hill, *Harris 11133* (F, NY, US). ST. ANDREW: Hardware Gap near New Castle, *Britton & Hollick 1806* (NY); Clydesdale to Chesterdale, vicinity of Cinchona, *Britton 334* (F, NY); Constant Spring to Bardowie, *Harris 12110* (F, GH, MO, NY, S, US); Port Royal Mts., Content Road, *Harris 5092* (US), *5263* (S, US); Lower Davids Hill, *Harris 5091* (C, US); Liguanea Hills, *Prior s.n.* (NY). ST. ANN: Union Hill near Moneague, *Howard 12031* (GH), *12022* (GH), *12013* (GH), *Prior s.n.* (NY); Mt. Diablo, *Hunnewell 19335* (GH). ST. CATHERINE: Holly Mount, *Harris 8901* (NY). ST. ELIZABETH: Malvern, *Britton 1195* (NY). ST. THOMAS: Bath, *Britton 3492* (NY), *Harris 6055* (F, NY); Green Valley, *Harris 5233* (C, NY), *12126* (F, GH, MO, NY, S, US); Mansfield, *Britton 3556* (NY); *Blue Mts., Harris 5274* (C, US), *5094* (B, BM) (Type of *Coccoloba neglecta*, C, J, US). TRELAWNEY: Oxford, *Britton 430* (NY); Troy, *Britton 919* (NY), *Harris 9094* (F, NY, US). WITHOUT SPECIFIC LOCATION: *Swartz s.n.*, TYPE (G, DC).

Bahamas: ABACO: *Brace 1481* (F, NY), *1697* (NY). BIMINI: South Bimini, *R.A. & E.S. Howard 10164* (GH, NY). CAICOS: North Caicos, *Wilson 7708* (F, GH, NY), *7744* (F, GH, NY). CROOKED ISLAND: *Brace 4658* (F, MO, NY, US). FORTUNE ISLAND: *Rothrock 264* (F, NY). GREAT BAHAMA: *Britton & Millspaugh 2544*, (F, NY), *2396* (F, NY). INAGUA: *Nash & Taylor 909* (F, NY), *1009* (NY), *1014*, (F, NY), *1428* (NY). LITTLE INAGUA: *Wilson 7769* (F, GH, NY). LONG ISLAND: *Britton & Millspaugh 6316* (F, NY); *Coker 520* (NY). NEW PROVIDENCE: *Britton & Brace 231* (F, NY), *324* (F, GH, MO, NY, US); *Britton & Millspaugh 2175* (F, NY); *Degener 18970* (A); *J.I. & A.R. Northrop 143* (F, GH, NY). ROSE ISLAND: *Britton & Millspaugh 2122* (F, NY, US); *Wilson 7900* (F, GH, NY).

Dominican Republic: PROV. PUERTO PLATA: *Wright, Parry & Brummel 472* (GH, US). ALTA GRACIA: *Taylor 414* (NY), *431* (NY, US), *433* (B, NY, US). DISTR. DE SANTO DOMINGO: San Isidro, *Ekman 11014* (S, US).

Puerto Rico: Lago San Jose: *Hioram s.n.* (NY); Maricao, *Sintenis 258* (B, GH, MO, NY, S, US); Dorado, *Britton, Britton & Brown 6741* (F, NY); Cayey to Aibonito, *Britton & Britton 9630* (NY); Monte Montoso, *Britton & Cowell 4125* (F, NY, US); La Estancita, *Eggers 1193* (US); Santurce, *Heller 4666* (A, F, GH, Mich., NY, US).

St. Croix: Salt River, *Thompson 580* (US); Sandy Point, *Raunkiaer 2508* (C); Jolly Hill, *Raunkiaer s.n.* (C); Mt. Eagle, *Thompson 427* (G, NY); Signal Hill, *Ricksecker 448* (F); Water Gut, *Isert s.n.*

Vieques Island: *Shafer 2733* (NY, US).

St. Jan: Mt. Eagle, *Ravn s.n.* (C).

Virgin Gorda: *Fishlock 126* (NY).

St. Kitts: Mt. Misery, *R.A. & E.S. Howard 11938* (GH).

Montserrat: Central Hills, *R.A. & E.S. Howard 11868* (GH), *11866* (GH), *11871* (GH), *11867* (GH), *11872* (GH); Gage's Upper Soufriere, *R.A. & E.S. Howard 11882* (GH); Gardru Gut, *Shafer 323* (F, NY, US), *615* (F, NY, US).

Antigua: Pearn Hill, *Box 975* (US).

Guadeloupe: Bois de Gombeyre, *Duss 3251* (F, GH, NY, US); Bouillante to Pont Noire, *R.A. & E.S. Howard 11843* (G).

Dominica: Salybia, *W. H. Hodge 3404* (GH); South Children Estate, *W. H. & B.T. Hodge 1583* (GH); Antilles near Magot, *R.A. & E.S. Howard 11754* (GH).

Martinique: Casa Pilote, *Hahn 1187* (F, GH, US), *R.A. & E.S. Howard 11712* (G); Trois Islets, *R.A. & E.S. Howard 11731* (GH); Montagnes des Trois Flotz, *Hahn 629* (F, GH); Presquile de la Caravalle, *R.A. & E.S. Howard 11727* (GH), *Egler 39–230* (NY); Mt. Pelee, *Duss* (NY); Diamant, *Duss* (NY).

St. Lucia: Castries-Dennery Road, *R.A. & E.S. Howard 11335* (GH), *11329* (GH), *11355* (GH); Vieux Fort, *R.A. & E.S. Howard 11404* (GH); Gros Piton, *R.A. & E.S. Howard 11506* (GH); Le Toc to Cul de Sac Bay, *R.A. & E.S. Howard 11377* (GH).

Barbados: Turners Hall Wood, *Eggers 7161* (US).

Coccoloba swartzii forma **pubescens** Howard, Jour. Arnold Arb. 30: 420. 1949.

The young shoots, petioles, the lower end of the upper leaf surface, especially on the midrib, the ochrea and the inflorescence rachis, at least at the base, puberulent to pilose pubescent.

Cuba: Oriente prov., Punta Padre, *Curbelo 224* (NY).

Guadeloupe: *De Ponthieu 86* (F).

Barbuda: Martello Tower, *J.D. Beard 372* (A, MO); Codrington Village, *Fairchild 3830* (A, US); *Box 602* (US).

Antigua: Sugar Loaf Mt., *Box 1543* (US), *1544* (US); Orange Valley, *Box 1184* (US); Blubber Valley, *Box 1411* (US, HOLOTYPE), *R.A. & E.S. Howard 11860* (GH), *11985* (GH), *11986* (GH); Pelican Bay area, *R.A. & E.S. Howard 11990* (GH); Carr's Ghaut, *R.A. & E.S. Howard 11994* (GH).

The validity of this form was questioned in its original publication, for at that time I had had little field experience with the group. In 1950 while doing field work in Antigua, considerable time and effort were spent investigating populations of this and other taxa of *Coccoloba* to determine distribution of plants, occurrence of pubescence and the interrelation of species reported from that area. *Coccoloba swartzii* proved to be a common plant on the dry hillsides throughout the island and one that was extensively cut for fuel and poles. It was represented in the full range of morphological variation found elsewhere and the growth forms produced by the influence of woodcutters allowed a full study of anomolous specimens earlier represented in herbarium specimens.

Coccoloba swartzii forma *pubescens* was particularly abundant as a dominant population on the hillsides in the Blubber Valley area. While the pubescent form was observed and collected in many other parts of the island, the extent and abundance of plants in all stages of development in Blubber Valley allowed special study. The pubescence used as the basis for this form was uniformly and characteristically developed on plants of this population. It was not associated, as had earlier been suspected, with teratological or adventitious shoots, juvenile plants, injuries or shade conditions. In the Blubber Valley area, mixing of the typical or non-pubescent form and the pubescent taxon did not occur. In fact, the non-pubescent plants appeared to occur only at the margins of populations of forma *pubescens* and the distribution suggested independent and not intermixing ranges.

The variations in growth of the pubescent form of *Coccoloba swartzii* duplicated those found in the species, as well as those found in other species. For example, the collection *R. A. & E. S. Howard 11990* was made from a tree just below the crest of a hill. Young, vigorous foliage occurred on the lower shaded branches and the leaves were predominantly ovate, acuminate to acute at the apex and cordate at the base. Their texture was thin. Some branches at the top of the tree were exposed to the sweep of the wind and these branches had more coriaceous leaves which were smaller in size and predominately orbicular in shape with rounded apices and rounded and only slightly cordate leaf bases. From the base of the same tree there were three adventitious shoots, two occurring normally and one definitely associated with a machete slash. These three shoots possessed leaves of similar appearance, delicate in texture, brightly colored, lanceolate-ovate in shape and three or four times the size of the foliage elsewhere on the plant. These three collections from different parts of the same tree, mounted on different herbarium sheets most certainly would have been referred to different species by previous workers.

Fruits of the pubescent plants were not abundant and seedlings or germinated fruits did not appear in the numbers encountered in the non-pubescent phase elsewhere. However, all seedlings examined from very young plants to saplings possessed a similar development of pubescence. Likewise, the oldest plants studied retained the pubescence on shoots, at least as long as the leaves remained. With the fall of the leaves the ochreae likewise disintegrate and the stems develop a corky layer with the loss of evident pubescence.

If *Coccoloba swartzii* forma *pubescens* were limited to Antigua, it would merit a varietal status on a geographic basis. It is, however, found on other islands and represented by occasional collections. A single collection by De Ponthieu from Guadeloupe must be referred to this form. Although I looked diligently in many areas of Guadeloupe, I was unable to locate any plants referable here. The range of the form is extended westward by one collection from the Oriente province of Cuba. It has also been collected on Barbuda.

Coccoloba swartzii forma **urbaniana** (Lindau) comb. nov.

Coccoloba urbaniana Lindau, Engler Bot. Jahrb. **13**: 155. 1890 in part, Symb. Antill. **1**: 225. 1899.

Coccolobis borinquensis Britton, Sci. Surv. P.R. **5**: 267. 1924.

Holotype: *Sintenis 1527* (GH).

Puerto Rico: Sierra de Naguabo, Loma Icaco, *Shafer 3448* (NY, type of *C. borinquensis*); *Britton, Britton & Cowell 207* (NY); Sierra de Luquillo, *Sintenis 1527* (F, GH, MO, NY, S, US), *Wilson 213* (F, NY, US), *Gregory 56* (NY), *Britton & Bruner 7665* (NY), *7676* (NY), *Barbour & Gerhart 9729* (NY); Indiera Baja, *Britton & Britton 7228* (GH, NY, US); Camp Dona Juaña, Villalba, *Gregory 64* (NY); Maricao Forest, *Sargent A-13* (US); *R.A. Howard 12602* (GH), *Winters 2213* (A).

Lindau described *Coccoloba urbaniana*, citing four collections, two by Crueger (*2694* & *2692*) from Trinidad and two by Sintenis (*1527* & *1585*) from Puerto Rico. His description, however, is obviously based on the material from Puerto Rico. No holotype was selected at the time. In his second publication of monographic studies on the genus *Coccoloba* in the Symbolae Antillanae, Lindau lists and keys *Coccoloba, urbaniana*, but cites only the Sintenis collections. In fact, the two Crueger collections are not cited anywhere in this publication. It appears that Lindau was, in practice, accepting the species *Coccoloba urbaniana* for Puerto Rico by excluding the Trinidad material.

Britton in 1924 described *Coccoloba borinquensis*, selecting *Shafer 3448* as the type specimen. He reports that this collection had been "erroneously included by Lindau in Coccoloba Urbaniana Lindau of Trinidad." The Shafer material was collected in 1914 and I can find no indication that Lindau saw the type specimen at the New York Botanical Garden or any duplicates or fragments of this collection. I can only conclude that Britton was referring to a misidentification and that he had overlooked the later Lindau reference which essentially limits the species to Puerto Rico.

Coccoloba borinquensis Britton has been considered endemic to Puerto Rico and has been collected many times, principally in the Luquillo Mountains and the Maricao National Forest. I have studied several populations of this plant in areas similar to mossy forests where it was most abundant. The species as recognized by Britton is a shrub, or rarely a small tree, and is characterized by anomalous and apparently teratological development of the inflorescence axis and the leaves. Both are enormously thickened in living condition and when dried as specimens. In many specimens the rachis thickens as the fruit develops, so that when the fruit falls, the pedicel is immersed in the fleshy axis tissue and the dried inflorescence axis appears to be deeply pitted. The anomalies in the collections cited are numerous. In collections by Sargent, Wilson and Gregory the axis varies in thickness along its length, being thin, almost tenuous at the base and swollen in the middle and at the apex. Many of the specimens in the collection by Sintenis are thickened and branched at the upper end.

One of the specimens collected by Gregory is flattened and obviously fasciated at the apex.

The leaves likewise show variation of an anomalous nature in both living condition and when dried. Many of the leaves seemed almost succulent when fresh, but thick and heavy rather than coriaceous when dry. The veins vary in the degree of prominence in the specimens cited, but such a character is not taxonomically reliable.

Populations of this plant seen in Puerto Rico and the collections on hand show a definite gradation of the characters Britton used to identify this species into the typical form of *Coccoloba swartzii*. However, the conspicuous nature of the abnormality in the field as well as in the herbarium makes it desirable to acknowledge these Puerto Rican populations as forms.

Meisner described with a query a variety of *Coccoloba swartzii* called var. *portoricensis*. Subsequent monographers and workers on the West Indian flora have been unable to place this taxon. Lindau in 1890 studied a drawing of the specimen Meisner cites and thought it might be related to *Coccoloba diversifolia* Jacq. (*C. laurifolia* Lindau) or *Coccoloba swartzii* Meisner (*C. diversifolia* or *C. barbadensis* Lindau). Meisner did not give the name of the collector and as Britton did not recognize *Coccoloba swartzii* Meisner from Puerto Rico Britton also was unable to associate the variety Meisner described with any other species. I have seen the Meisner material at the De Candolle Herbarium in Geneva. It was collected by C. G. Bertero in 1820. A portion of this collection appears in the material I have on loan from the Missouri Botanical Garden herbarium. The Bertero material typifying *C. swartzii* var. *portoricensis* is intermediate between the anomalous *C. swartzii* forma *urbaniana* and the typical *C. swartzii*. It is easily matched by material from the Dominican Republic collected near Puerto Plata and specimens from Seibo by other collections from Puerto Rico and by some from Jamaica. *Coccoloba swartzii* var. *urbaniana* intergrades through material such as *Coccoloba swartzii* var. *portoricensis* into typical material of *C. swartzii*. The transition is so gradual and yet so complete throughout a number of collections that it is impossible to recognize the Meisner variety as a valid taxon.

Coccoloba × boxii, stat. nov. (or *Coccolobis boxii* Sandwith, Jour. Bot. 78: 97–98. 1940.)

Tree to 8 m. tall; current year's branches cinereous, striate, sulcate, pubescent; ochrea to 1.5 cm. long, densely pubescent, the base persistent, sub-coriaceous, the apex membraneous-evanescent; leaves cordiform-ovate, 11 × 6.5 cm. long, 27 × 17.5 cm. broad, coriaceous, light, midrib pubescent; lateral veins 8–12, slightly prominent; petiole densely pubescent, 0.7–1.3 cm. long; apex obtuse, the base oblique, auriculate-cordate or rounded to nearly evenly cordate; inflorescence solitary, simple, 17–22 cm. long; rachis 1.5–2 mm. wide, sulcate, densely minutely pubescent, nodules 1–4 flowered, the bracts broadly triangular-ovate, rounded-obtuse, 1.3 mm.

long, 2 mm. wide, conspicuously pubescent, the ochreolae 2 mm. long, membranaceous, flaring, almost bilobed, glabrous at the base; pedicels to 0.75 mm. long, the hypanthium 1.3 mm. long, the perianth lobes ovate-obtuse, 2 mm. long, 1.75 mm. broad, the interior smaller, the filaments (in bud) 0.6 mm. long; ovary ovoid-ellipsoidal 2.3 mm. long, 1.3 mm. in diameter, glabrous; styles shorter than ovary about 0.75 mm. long.

Antigua: Pelican Bay, *Box 539* (BM, US), *1497* (HOLOTYPE — BM, US).

In the original description of this species Mr. Sandwith reported, "Mr. Box writes that there was only a single tree, about 25 feet high, in this locality, but that he has noted others which appear to be conspecific in a few other stations in the central region of Antigua, *e.g.*, near Piccadilly and at English Harbour. It is a small, much stunted and distorted tree, presenting characters which would suggest a hybrid between *C. diversifolia* and *C. uvifera*, both of which grow in the coastal thickets at Pelican Bay. The tree is easily recognized in the field by the broadly cuspidate-acuminate leaf which somewhat resembles that of the Jamaican *Coccoloba litoralis* Urb."

"It is possible that *Coccolobis Boxii* may represent a hybrid between *C. diversifolia* and *C. uvifera*. The latter species would contribute to such characters as the thicker branchlets with persistent bases of the ochreae, the deeply cordate base of the larger leaves, their venation and texture, the shortly pedicellate flowers, and, perhaps, the indumentum of the branchlets, ochreae and the rhachis of the inflorescence. It is unfortunate that the male perianths have all fallen, and that it is impossible to estimate the length of their pedicels. Again, there are no fruits present on the material, but the single ovary that was dissected bore an apparently healthy ovule. I do not think that the evidence for treating this very distinctive-looking plant as a hybrid is quite conclusive, and prefer to describe it provisionally as a new species."

On the labels Box has indicated that collections *539* and *1497* are from the same tree, although at different times, the former in February and the latter in July. Box also reported that this tree was growing on the seashore with *C. uvifera* and his collection *975* which is *C. swartzii* (*C. diversifolia* Sandwith).

In 1950 I visited the Pelican Bay area of Antigua in the hope of locating the specific plant from which Box had collected the material cited above. In addition to specimens of *Coccoloba uvifera* and *C. swartzii*, I also found the pubescent form which I had described previously, *C. swartzii* forma *pubescens*. Careful study was given to all the plants seen, but I was unable to locate a tree answering to Box's description or which would yield specimens to match the type collections.

Sandwith had seriously considered the possibility of hybrid origin of these plants and, as reported above, decided that the evidence was not conclusive and so described the species provisionally. He further stated in the opening paragraph of his paper that "there is a possibility of hybrid origin. I have been unable to trace any evidence of hybridity between

species of this large genus, but this is not surprising when we consider how rarely hybrids are recorded from the tropics, although there is no reason to suspect that they occur less frequently there than in temperate regions where they become a favorite *deus ex machina* for the solution of botanical difficulties. Only the prolonged residence in tropical countries of such careful and enthusiastic observers as Mr. Box will enable the taxonomist to deal satisfactorily with variable and critical plants collected in those areas."

The taxonomist who proposes a hybrid origin for the species in question is put on the defensive by Mr. Sandwith's comments. However, several factors now count in the writer's favor. In 1940 when Mr. Sandwith wrote, no hybrids were recognized in the large and complex genus *Coccoloba*. Now many are recognized, including *C. jamaicensis* (*litoralis*), which Sandwith reports resembles *C. boxii*. The genus had not been monographed nor had it received intensive study for about forty years. For the past five years, however, the present writer has been studying the group intensively in the laboratory and in the field and has searched in the area under discussion for the answers to the questions raised by Mr. Sandwith.

It is apparent to me that the two collections cited in the original description of *Coccolobis boxii* coming from one tree represent a single hybrid plant. No collections have been made since then which can be referred to this hybrid species. The parents of the plant upon which this species is based are *C. uvifera* and either *C. swartzii* or *C. swartzii* forma *pubescens*. My feeling is toward the latter, although both *C. swartzii* (*Box 975*) and *C. swartzii* forma *pubescens* (*R. A. & E. S. Howard 11990*) have been collected in the area of Pelican Bay.

Sandwith reported that Box had noted other specimens in the central region of Antigua near Piccadilly and at English Harbour which appear to be conspecific with the plant described. These observations, however, are not supported with voucher specimens and it is my suspicion that Box observed the adventitious shoot leaves of *C. swartzii* forma *pubescens* in these areas. Collections made at Blubber Valley (*R. A. & E. S. Howard 11864* & *11865*) and at Carr's Ghaut (*R. A. & E. S. Howard 11994*) of both adventitious shoots and normal growth show the difference to be expected on one plant. The leaves of the adventitious shoots of *R. A. & E. S. Howard 11994*, in particular, could be included in the concept of *C. boxii* if they had not been collected, personally and carefully, along with the normal foliage from another part of the same plant. The leaves of adventitious shoots of the collection *11864* are slightly more ovate than those of *Box 1497*, but are supported by fruiting branches bearing the small leaves typical of *C. swartzii* forma *pubescens*. A plant collected in sterile condition in Blubber Valley (*R. A. & E. S. Howard 11865*) has on one branch leaves which are a perfect match for *C. boxii* and *C. swartzii* forma *pubescens*.

The specimens collected by Box and the species described by Sandwith are retained as *C. boxii*, although a hybrid status is now recognized for this single plant. Sandwith described the flowers as pistillate and felt that

staminate flowers had fallen. I feel that the Box specimens represent staminate flowers, although only young buds are present and it is difficult to predict the fertility of either pollen or ovule in the stages present. The clusters of flowers are characteristic of functionally staminate plants and the fact that Box was unable to find fruits or fruiting pedicels on the plant in either February or July is indicative of a functionally staminate plant. The striations and general aspect of the branches, the size of the ochrea, the shape of the leaf and its texture and color, as well as the length of the inflorescence, are indicative of parentage involving *C. uvifera* and prevent these collections from assignment to *C. swartzii*.

Coccoloba microstachya Willd. Sp. Pl. **2**: 459. 1800; Lindau, Engler Bot. Jahrb. **13**: 146. 1890.

Coccoloba klotzschiana Meisn. DC. Prodr. **14**: 155. 1856; Lindau, Engler Bot. Jahrb. **13**: 148. 1890.

Coccoloba microstachya var. *ovalifolia* Meisn. DC. Prodr. **14**: 162. 1856.

Coccoloba parvifolia Poir. in Lam. Encycl. **6**: 64. 1804.

Coccoloba microstachya var. *rotundifolia* Urban ex Lindau, Engler Bot. Jahrb. **13**: 147. 1890.

Coccoloba microstachya var. *lanceolata* Meisn., DC. Prodr. **14**: 162. 1856.

Coccoloba obtusifolia Lindau, Symb. Antill. **1**: 222. 1899, Britton & Wilson, Sci. Surv. P.R. **5**: 268. 1924, not Jacquin.

Coccoloba punctata Griseb. in part, Flora Brit. W.I. 163, 1859, not Linnaeus.

Shrub or tree to 20 ft. tall; branches terete, the nodes tumid, pubescent or with hair primordia, the bark gray to tan in color; ochrea membranaceous, cylindrical, pubescent, 4 mm. long; petioles 3–6 mm. long, flattened above, normally pubescent; blades variable in size and shape, ovate, ovate-lanceolate, oblong or elliptic, 3.5 × 1.5, 4 × 2, 5.5 × 3.5 to 7 × 4 cm. long and broad, thin-coriaceous, usually turning black on drying, the margin entire, often undulate, sometimes tightly recurved; midrib and veins prominulous on both surfaces, forming a dense reticulum, although blades relatively thick and often somewhat fleshy in fresh condition, the veins 7–9 pairs, prominent or numerous and all equal and less conspicuous, straight or arcuate, curved and anastomosing at the margin; glabrous above, pilose or glabrate below, occasional hairs remaining on the veins or rarely the entire leaf surface persistently pubescent; apex acute, acuminate rounded or emarginate, the base narrowed, rounded or slightly cordate; leaves of adventitious shoots ovate-lanceolate, 10.5 × 5.5 to 16.5 × 5 cm. long and broad on petioles 7 mm. long with ochrea 8 mm. long, the adventitious leaves cordate at the base, generally tapering or acuminate at the apex and often conspicuously puberulent below; inflorescence terminal, 5–10 cm. long, the rachis usually pubescent, tenuous, rarely stout, often geniculate, commonly recurved; staminate flowers two, rarely one or more than two at the nodes; pistillate flowers solitary, the bracts broadly ovate, 0.5 mm. long, puberulent; ochreolae membranaceous, puberulent, to 0.5 mm. long, erect and surrounding the flower in the staminate plants, gen-

erally appressed or flattened against the rachis in the pistillate plants in flower and fruit, pedicels none or shorter than the ochreolae, the hypanthium less than 1 mm. long, the perianth lobes 1–1.5 mm. long and 1 mm. wide; fruit sessile, generally ovate with distinctly coronate perianth lobes, to 6 mm. long and 4 mm. in diameter.

Dominican Republic: PROV. SAMANA: Samana, *Ekman 15322* (B, S), Cabo Samana, *Ekman 14905* (S). PROV. PUERTO PLATA: La Boca, *Ekman 14381* (S, US), Arroyo Frances, *Ekman 14400* (S, US), Puerto Plata, *Eggers 2674* (B). PROV. MONTE CRISTI: El Morro, *R.A. & E.S. Howard 12537* (GH). PROV. UNKNOWN: Castillo Maldonado, *Sesse & Mocino 951* (F).

Puerto Rico: GUAYANILLA: *Britton & Shafer 1817* (F, GH, NY, MO, US); *Sintenis 4868* (MO, US). GUANICA: *Britton & Britton 9594* (S); *Sintenis 3707* (B), *3431* (MO, US); *Gregory 181* (NY); *Holdridge 181* (A). MAYAGUEZ: *Heller 4546* (A, B, E, F, GH, NY, Mich, MO, NY, US); *Britton, Cowell & Brown 4359* (NY, US); *Britton & Hess 2715* (F, NY, US). PONCE: *Heller 6128* (A, E, F, GH, MO, NY, US); *Underwood & Griggs 686* (NY, US). CABO ROJO: *Sintenis 545* (GH, S, US), *Velez 1096* (NY). CAYO MUERTOS: *Britton, Cowell & Brown 4999* (NY). PUNTA GUANIQUILLA: *Britton, Cowell & Brown 4566* (F, GH, NY, US), *4573* (NY, US). RINCON: *Sintenis 5498* (F, NY), *5543* (E, F, NY). COAMO: *Sintenis 3328* (E, GH, S, US). PEÑON: *Shafer 1985* (NY, US). CERRO VENTANA: *Shafer 2976* (NY, US). SANTA MARIA to CABALLO COLORADO: *Shafer 2689* (NY, US). ENSEÑADA HONDO: *Britton & Britton 9645* (NY). CULEBRA ISLAND: *Britton & Wheeler 8A* (NY, US), *32* (F, NY, US). MONA ISLAND: *Stevens 6170* (NY), *6213* (NY); *Britton, Cowell & Hess 1710* (NY). VIEQUES ISLAND: *Shafer 2805* (NY, US).

St. Thomas: Bolongo Hill, *Eggers 160* (C, S). Flaghill: *Eggers s.n.* (US). Bordeaux: *Britton & Marble 1378* (C, F, NY, US); *Ostenfeld 328* (C), *330* (C). WITHOUT SPECIFIC LOCATION: *Eggers 135* (B), *124* (GH), *714* (A); *Britton, Britton & Shafer 159* (C, F, NY, US); *Paulsen 146b* (NY). COLLECTOR NOT SPECIFIED: Herb. Kunth, TYPE of *C. klotzschiana*.

St. Jan: Bethania, *Britton & Shafer 192* (NY, US); Solomon's Bay, *Eggers 3314a* (C).

Tortola: *Fishlock 124* (F, NY).

Virgin Gorda: *Fishlock 20* (GH, NY), *279* (GH, US).

Anguilla: *Boldingh 3483b* (NY).

St. Croix: Oxholmia: *Borgesen 64* (C); Fair Plains, *Eggers s.n.* (C); Kingshill *Eggers s.n.* (C); Salt River, *Paulsen 264* (C); Folly Hill, *Raunkiaer s.n.* (C); Rustup Twist, *Mrs. J.J. Ricksecker 365* (F, MO, US); Salt River Cliff, *A.E. Ricksecker 459* (F, GH, MO, NY, US); Christiansted, *Rose Fitch and Russell 3582* (NY, US); Anna's Hope, *Thompson 398* (GH, NY); Mt. Eagle, *Thompson 434* (GH, NY).

A large number of specimens have been seen which were collected by Ryan, Benson, Krebs, Eggers, Swartz, Borgesen and others which lack either locality and are cited as "Ind. Occ." or lack collector's numbers, as well. Little is gained in attempting to cite these specimens which are primarily from the herbaria at Stockholm and Copenhagen. The two specimens in the Willdenow Herbarium in Berlin are *7703*, the type of the species, and *7702*, the type of *C. microstachya* var. *lanceolata* Meisner.

Both are probably from St. Croix and were probably collected by Vahl. Although Lindau listed four Sintenis collections from Puerto Rico, he failed to cite a type when he described *C. microstachya* var. *rotundifolia*.

The holotype of this species is *Willdenow 7703* in the Willdenow Herbarium in Berlin. In his original monograph of this genus, Lindau accepted *Coccoloba microstachya* Willd. and recognized three varieties. *Coccoloba microstachya* var. *ovalifolia* was described earlier by Meisner and included the holotype. *Coccoloba microstachya* var. *lanceolata* was described also by Meisner. Lindau describes a variety *rotundifolia* attributed as a manuscript name by Urban. In the synonymy of *C. microstachya* var. *ovalifolia*, Lindau cites *C. obtusifolia* Jacquin.

In a later treatment of the genus for the West Indies (Symb. Antill. 1: 222. 1899), Urban recognized the earlier publication of the Jacquin name *Coccoloba obtusifolia* and, accepting this as the correct name for the species, listed in synonymy *C. microstachya* and the three varieties recognized in his earlier publication. The rejection of the morphological varieties is based on a better understanding of the variation within this species and particularly within the development of an individual plant. I agree with Lindau's concept of the morphology of the species, but cannot agree with his acceptance of the name *C. obtusifolia* Jacquin. The description and illustration of the plant Jacquin considered *C. obtusifolia* is clearly not the same plant called *C. microstachya* and typified by the Willdenow specimens. Further, *C. obtusifolia* Jacquin is based on a plant from Carthagena in Colombia. This is the plant which Lindau describes as *C. billbergii* (Engl. Bot. Jahrb. 13: 219. 1890) and this species is not known from the West Indies.

Although Willdenow described *Coccoloba microstachya* as having glabrous leaves and stems, the type specimen in the Willdenow herbarium shows a minute but distinct pubescence. In the large number of specimens examined in the herbarium and in the field, the amount and the evidence of the indument varies. The pubescence is often represented only by bases of hairs recognized as clear, lighter colored dots or cells in the epidermis of the dried leaves. Generally a slight pubescence remains on the rachis of the inflorescence and is evident when all other portions of the specimen are glabrous. The extreme in foliar pubescence was seen on a specimen collected by Boldingh (*3483B*) from Anguilla where the lower leaf surface of the mature foliage was almost tomentose.

The variation in leaf shape is great, not only in populations but in individual plants. The three taxa which Lindau recognized in 1890, as he reported later, can be found on a single plant or in a single collection. Within the fourteen sheets of the four Sintenis collections that I have examined, all three varieties can be recognized. Some of the herbarium specimens cited seems to have been selected deliberately in the field to show gross and exaggerated variations. The largest adventitious leaves are on the specimens from St. Croix and many of the collections consist only of such shoots and leaves. However, a Britton & Wheeler collection (*32*) shows both the large leaves of the adventitious shoots as well as the smaller

leaves, presumably of the same plant although no mention is made of this in the field notes. An Ekman collection (*14381*) from Puerto Plata in the Dominican Republic also has fragments from adventitious and normal shoots and the relationship of these is mentioned on the label. An earlier collection by Ekman (*12098*) from La Romana in the Dominican Republic consisted primarily of leaves from adventitious shoots and the annotation that such a plant was "very rare and not seen elsewhere."

Several specimens from St. Croix show an almost teratological thickening of the inflorescence axis. While this is common in other species, and particularly in *Coccoloba swartzii*, it appears unusual in *C. microstachya*.

Coccoloba parvifolia Poir. is based on a Vahl collection and the type is in the Jussieu Herbarium. I have examined a photograph of the type sheet and agree that this species can be referred to the synonymy of *Coccoloba microstachya* Willd. Meisner, however, recognized this species and considered it an "obscure" species from South America. However, the Vahl collection is probably from St. Croix.

The type specimen of *Coccoloba klotzschiana* in the De Candolle Herbarium at Geneva and the fragment of this in the herbarium of the New York Botanical Garden indicate this species may also be referred to *C. microstachya*.

In the extreme forms of *Coccoloba microstachya*, it is difficult to distinguish between this and *C. swartzii*. Usually, however, *C. swartzii* may be recognized by the larger leaves, longer and thicker inflorescence axes, tapered fruit with imbricated perianth lobes, the lack of pubescence (except in forma *pubescens*) and the darker, almost black color of the leaves when dry. By comparison, *C. microstachya* has smaller leaves, tan to brown in color rather than black, exaggerated tumid nodes, shorter and more tenuous inflorescences and fruit with coronate perianth lobes.

Coccoloba pyrifolia Desf. Cat. Hort. Paris ed. 3, 69, 389. 1829.

Coccoloba pirifolia Lindau, Engl. Bot. Jahrb. **13:** 144. 1890, Symb. Antill. **1:** 222. 1899.

Coccolobis pirifolia Lindau, Brit. & Wils. Sci. Surv. P. R. **5:** 267. 1924.

Coccoloba kunthiana Meisner, DC. Prodr. **14:** 166. 1857.

Coccoloba punctata var. *jacquini* Griseb. Fl. Brit. W.I. 163. 1859.

Shrub of 9 ft. to a tree of 30 ft.; trunk to 14 inches diameter at breast height; branches striate, glabrous, the nodes not conspicuously swollen; ochrea subcoriaceous, glabrous, shriveling rather than deciduous, 1 cm. long; petioles inserted below the ochrea, glabrous, 0.6–1.5 cm. long; blade ovate-lanceolate, broadly ovate or occasionally completely orbicular, 4.5 × 2.5, 9 × 5, 12 × 6, cm. long and broad, coriaceous, glabrous, opaque to almost shining, the margin entire, sometimes recurved, the midrib slightly evident below, prominent above, the primary veins flat, slightly impressed above, very slightly evident below, the secondary venation obscure, the apex obtuse, acute or rarely acuminate, the base rounded, narrowed or subcuneate; inflorescence terminal, spike-like, 1–2 times the length of the

leaf or terminal on lateral shoots, 8 to 31 cm. long, glabrous, the staminate and pistillate flowers borne singly, the bracts triangular to 1.5 mm. long, the ochreolae membranaceous, equalling the bracts; pedicels wanting; hypanthium 1 mm. long, the perianth lobes ovate, to 2 mm. long, the filaments of fertile stamens 3 mm. long; fertile pistil to 2.5 mm. long; fruit globose, ca. 4 mm. in diameter, rounded at the base, obscurely 3-angled, the perianth lobes coronate, laxly acuminate; achene tan in color.

Puerto Rico: MAYAGUEZ: *Cowell 730* (F, US), *731* (F, NY, US); *Otero & Alvarez 540* (A, F); *Sintenis 1018* (BM, US); *Heller 4560* (A, E, F, GH, Mich., MO, NY, US). SIERRA DE LUQUILLO: *Sintenis 1405* (F, MO, S), *1501* (BM, GH, NY, US); *Britton & Bruner 7551* (NY). SANTURCE: *Heller 614* (F, NY, US), *1259* (F, NY), *1268* (NY, US). LA ESTANCITA: *Eggers 1173* (US). MT. ALEGRILLO: *Britton, Stevens & Hess 2572* (F, MO, NY, US); *Sintenis 238* (GH, MO, S, US); *Hess 645* (NY). VEGA ALTA: *Britton, Britton & Brown 6796* (F, NY, LECTOTYPE, US). CAMUY: *F.H. Sargent B-200* (US). GUAYAMO: *Britton, Britton & Brown 6544* (F, NY, US). MARTIN PENA: *J.R. Johnston 1867* (NY, US). MT. MORALES: *Britton & Marble 1058* (NY, US). MARICAO: *F.H. Sargent 397* (US). BAYAMON: *Sintenis 990* (BM, GH, US); *Britton, Britton & Boynton 8455* (GH, NY, US). LAGO SAN JOSE: *Hioram 372* (NY). VEGA BAJA: *Stevens 1932* (NY). YAUCO: Indiera Baja, *Britton & Britton 7227* (NY). CAYEY: *Otero 730* (A, NY). ESPINOSA above Toa Baja: *Britton & Britton 9709* (NY). SAN JUAN: *Gerhart & Holdridge 536* (NY). CATANO: *Britton, Britton & Brown 6980* (NY). SIERRA DE NAGUABO: *Shafer* 3480 (NY). TORO NEGRO, Doña Juana: *Gregory 54* (NY).

Coccoloba pyrifolia Desfontaines was described in the third edition of the catalogue of plants in the botanic garden at Paris and was based on material under cultivation there. The origin of the plant is given as the warmer Antilles. No holotype exists for this species and no lectotype has been selected, to the best of my knowledge. There is in the herbarium at Geneva a specimen without collector's name or date, bearing a label indicating its origin as "hort. paris." It is possible that this specimen represents the original material cultivated and described in 1829 and could possibly be considered as the type. It seems more desirable to select a new lectotype from more recent collections and so *Britton, Britton & Brown 6796* is designated the type collection, with the holotype at the New York Botanic Garden herbarium. The species has been reported from Puerto Rico, St. Thomas, Cuba and Jamaica. I have seen the collections which Lindau cited from the herbaria at Berlin and Göttingen and there are currently no collections from St. Thomas. Lindau's reference to the occurrence of this species on St. Thomas cannot be checked. Likewise the Wilson specimen from Jamaica which Lindau states is in the Grisebach Herbarium cannot be located. Fawcett & Rendle repeat this reference which cannot be verified. The two collections by Charles Wright from Cuba which Sauvalle refers to this species in his Flora Cubana (139. 1873) are *Wright 2253* which is *Coccoloba praecox* Wright ex Lindau and *Wright 2256* which is the type of *C. reflexa* Lindau. It appears that *C.pyrifolia* is currently limited to Puerto Rico. The original spelling of the specific

name is retained in this treatment, although all recent authors have preferred to use *Coccoloba pirifolia*.

Meisner's original description of *Coccoloba kunthiana* contains few diagnostic characters and is clearly referable to the synonymy of this species. I have seen specimens in the De Candolle Herbarium on which Meisner's species is based and conclude the differences recognized by various authors in the past have been primarily of growth characters. The plants with older and shorter compacted branches are named *C. kunthiana* and are similar to Meisner's type. These specimens also have smaller ovate leaves which are generally obtuse at the apex. Specimens from obviously faster growing shoots have larger leaves which are acute or acuminate at the apex and possess longer inflorescences. These specimens, almost without exception, have been referred to *C. pyrifolia*. It is quite clear from a study of the material cited and from a field knowledge of the species that only a single taxon is represented and that the larger acute leaves are produced on adventitious or vigorously growing shoots.

Coccoloba pyrifolia is easily recognized by the long thin inflorescences with sessile flowers. It is most easily distinguished from *C. swartzii* by having leaves which dry dark brown and almost shiny above and light brown or tan beneath and which have very inconspicuous venation.

Coccoloba krugii Lindau, Engl. Bot. Jahrb. 13: 145. 1890, Symb. Antill. 1: 222. 1899.

Coccoloba børgesenii Schmidt, Fedde Repert. Sp. Nov. 24: 75. 1927.

Coccoloba børgesenii forma *ovato-lanceolata* Schmidt, Fedde Repert. Sp. Nov. 24: 76. 1927.

Shrub or small tree to 6 m. tall; branches terete, glabrous, slightly geniculate and nodose; ochrea membranaceous, persistent, 3–5 mm. long; petioles borne at the base of the ochrea, corky at the base, 5–6 mm. long; blade ovate to suborbicular 2 × 1.8, 4 × 3.5, 5 × 4 cm. long and broad, thin-coriaceous, glabrous or rarely with a few hairs near the attachment of the petiole, the margin flat or recurved, the midrib flat above slightly prominent below, the primary veins 4–6 pairs, straight, bifurcating and anastomosing near the margin, flat on both surfaces, the secondary venation minutely reticulate below, smooth above, the apex obtuse or rounded, the base cordate or rounded; adventitious leaves from the base of the ochrea 1 cm. long with petioles 1 cm. long and blades cordate or elliptic to 7 × 6 cm. long and broad; inflorescence terminal, 5–8 cm. long, rachis glabrous, the staminate flowers 1–3 per node, the pistillate flowers borne singly, the bracts broadly ovate, membranaceous, 1 mm. long; ochreolae membranaceous, flaring to 1 mm. long; pedicels wanting or shorter than the ochreolae, the hypanthium 1 mm. long, the perianth lobes ovate, to 2 mm. long, the filaments of fertile stamens 1.5 mm. long; fruit ovoid or angularly fusiform, strongly triangular in outline, 4–5 mm. long, 3–3.5 mm. in diameter, the perianth lobes appressed, above half the length of the fruit.

LOCAL NAMES: Cragwood (Bahamas); Wild Grape (Virgin Islands).

Bahamas: ACKLIN'S ISLAND: *Eggers 3960* (B, US); *Brace 4387* (FM, NY, US), *4495* (FM, NY). ANDROS: *Brace 5235* (FM). CAICOS ISLANDS: S. Caicos, *Wilson 7594* (FM, G, NY); W. Caicos, *Wilson 7754* (MF, G, NY); Dellis' Cay, *Millspaugh 9225* (FM, G, NY). CAT. ISLAND: Fort Hine, *Britton & Millspaugh 5948* (FM, NY); The Bight, *Britton & Millspaugh 5917* (FM, NY); Orange Creek, *Britton & Millspaugh 5779* (FM, NY); Port Hower, *Hitchcock s.n.* (MO). CROOKED ISLAND: *Brace 4748* (FM, NY); *Hitchcock s.n.* (FM, G, NY). FORTUNE ISLAND: *Eggers 3801* (US), *3998* (US); *Rothrock 261* (FM, G, NY). INAGUA: *Nash & Taylor 1059* (FM, NY), *968* (FM, NY); *Hitchcock s.n.* (MO). LONG CAY: *Brace 4040* (FM, NY, US). NEW PROVIDENCE: *Britton & Brace 361* (FM, NY), *363* (FM, NY, US), *364* (FM, NY), *372* (FM, NY), *375* (FM, NY); *Curtis 71* (A, FM, G, MO, NY, US). WATLING'S ISLAND: *Britton & Millspaugh 5194* (NY); *Coker 473* (NY); *Wilson 7215* (FM, G, MO, NY), *7324* (FM, G, MO, NY).

Haiti: Tortue, Morne Barranca, *Ekman 4314* (TYPE of *C. børgesenii*, S, US); Port au Paix, Valle des Trois Rivieres, *Ekman 3588* (TYPE of *C. børgesenii* forma *ovato-lanceolata*, S, US); Port au Paix, *E.C. & G.M. Leonard 15252* (A, G, US).

Dominican Republic: Prov. Monte Cristi: El Morro, *Ekman 13143* (S), *R.A. & E.S. Howard 12532* (G), *12534* (G).

Jamaica: ST. ANDREW: Long Mt. on road to Wareka, *Harris 10008* (FM, NY, US), *10014* (FM, NY, US), *Maxon 10521* (G, NY, S, US), Long Mt., *Howard 12033* (G). ST. CATHERINE: Great Goat Island, *Harris 9335* (A, FM, NY, US). ST. ELIZABETH: Lovers Leap, Santa Cruz Mts., *Britton 1149* (NY). ST. THOMAS: Albion Mt., *Harris 11680* (FM, G, MO, NY, US), *11681* (FM, G, MO, NY, US). TRELAWNEY: Ramgoat Cave, *Howard & Proctor 14392* (A), *Howard, Proctor & Stearn 14683* (A).

Puerto Rico: Guanica near Salinas, *Britton, Britton & Boynton 8314* (NY); Guanica in woods on Monte Cobana, *Sintenis 3776* (MO, NY); *Ponce, Underwood & Griggs 673* (NY, US); *Heller 6211* (A, FM, GH, MO, NY, US); *Britton & Cowell 1289* (NY, US); Icacos Cay, *Britton 7153* (NY); Vieques Island, *Shafer 2785* (NY, S, US); Guayanilla, *Britton & Shafer 1841* (F, MO, NY, US).

Anagada: *Fishlock 26* (NY), *27* (NY); *Britton & Fishlock 1001* (NY), *1063* (F, NY, MO, US), *J. Beard 323* (A).

Antigua: Frecetown, *Box 845* (US); Goble Creek near Gaynors, *Box 1388* (US).

Barbuda: *Fairchild 3829* (A, US).

St. Martin: *Boldingh 2756B* (NY).

There is little reason to confuse *Coccoloba krugii* and *C. swartzii*, although such errors of identification are relatively common on herbarium sheets. The smaller rounded leaves, light in color with short, pale gray petioles, distinguish *C. krugii* in sterile and flowering condition. The smaller and distinctly triangular fruits of *C. krugii* are equally characteristic.

Coccoloba børgesenii was described by Schmidt as having a puberulent inflorescence rachis. This "puberulence" on the type specimen appears to be a mixture of fungal hyphae, crystals of mercuric bichloride and fibers from the pressing material. The type specimen of *C. børgesenii* forma *ovato-lanceolata* consists of a vigorously growing shoot with larger leaves

than the species and again represents the difference between adventitious shoots and normal growth.

All of the characters Schmidt uses to separate this species and its form are expected variations present in *Coccoloba krugii*.

Lindau based the original description of *Coccoloba krugii* on two collections of Sintenis (*3497*, *3776*) from Puerto Rico and two collections of Eggers from Fortune and Acklins Island (*3801*, *3960*). No holotype has been selected and a lectotype should be designated. The Sintenis collection 3497 in the Berlin Herbarium should be so considered. In recent years *C. krugii* has been collected on additional islands of the Bahamas, on Jamaica, Haiti and the Dominican Republic, several islands of the Virgin Island group and Antigua of the Leeward Islands.

Coccoloba leonardii Howard, Jour. Arnold Arb. **30**: 419. 1949.

This species was based on a specimen collected by E. C. and G. M. Leonard on Tortue Island, Haiti. In the original publication additional material was cited from Haiti proper, Navassa Island and Cuba. I have not seen any additional material in recent collections which can be referred to this species.

Coccoloba leonardii is closely related to the polymorphic *C. swartzii*, but is readily distinguishable in fruiting condition by having fusiform, bicolorous fruits which are larger than those of *C. swartzii* from the Greater Antilles. The flowering spikes of *C. leonardii* appear more tenuous and often tortuous in comparison with the majority of specimens of *C. swartzii* and the striking asymmetry of the leaf base combined with a characteristic ashen color of the dried leaves appears to distinguish this species in sterile condition, as well.

A MONOGRAPHIC STUDY OF THE WEST INDIAN SPECIES OF PHYLLANTHUS *

GRADY L. WEBSTER

With two plates

SYSTEMATIC TREATMENT

IN THE FOLLOWING PAGES are treated all of the species of *Phyllanthus*, whether spontaneous or cultivated, which have been observed in the West Indies. For the purposes of this study the West Indian region is defined as the area bounded by (and including) Bermuda and the Bahamas on the north, Swan Island and the Providenciales on the west, and Curaçao, Trinidad, and Tobago on the south; the Florida Keys, as well as Margarita and the smaller islands off the Venezuelan coast, are therefore excluded. The inclusion (for reasons of convenience) of Trinidad, which has a predominantly South American flora, results in the mustering in of two species which are otherwise South American; but by and large the species here included represent a strikingly self-contained assemblage for such a large and diverse area, encompassing as it does a broad range of latitude and great diversity of climates, geological formations, and vegetational zones.

One of the most troublesome problems which faces anyone who wishes to investigate a West Indian *Phyllanthus* is that of deciding if the plant at hand actually belongs to the genus. The following purely artificial key to the West Indian representatives of Phyllantheae is therefore presented with the aim of facilitating determination. It should be noted that the tribe Phyllantheae is here circumscribed in a narrow sense, comprising the subtribe Phyllanthinae and part of the Andrachninae of Pax (Natürl. Pflanzenfam. ed. 1, 3(5): 14. 1890), or the subtribes Glochidiinae, Phyllanthinae, Andrachninae, and Wielandiinae of Pax and Hoffmann (Natürl. Pflanzenfam. ed. 2, 19c: 32–33. 1931). It is evident that further research will result in interpretations of the tribes and subtribes radically different from the arrangement of Pax and Hoffmann.

ARTIFICIAL KEY TO WEST INDIAN GENERA OF PHYLLANTHEAE

A. Plants in flower

1. Branching phyllanthoid ..... **Phyllanthus**
1. Branching not phyllanthoid.
   2. Petals present, at least in male flower; stamens 5.
      3. Monoecious subshrub, microphyllous, the leaves only 1–2 mm. long ..... **Andrachne**
      3. Dioecious shrubs or trees with much larger leaves.
         4. Petals about as large as the calyx-lobes; pistillode peltate; petiole c. 2 cm. long or more ..... **Astrocasia**

* Continued from volume XXXVII, page 268.

4. Petals much smaller than calyx-lobes; pistillode slender, usually lobed; petioles much shorter ..... **Savia**

2. Petals absent.

3. Pistillode present, stamens 5; dioecious shrubs or trees.

4. Male flowers subsessile, glomerate; leaves chartaceous, triplinerved, narrowly peltate ..... **Chascotheca**

4. Male flowers pedicellate; leaves coriaceous, pinnately nerved, never peltate ..... **Securinega**

3. Pistillode absent.

4. Stamens 4; floral disk annular; dioecious tree ..... **Margaritaria**

4. Stamens 3; floral disk not annular; monoecious or dioecious herbs or shrubs ..... **Phyllanthus**

B. Plants in fruit

1. Branching phyllanthoid ..... **Phyllanthus**

1. Branching not phyllanthoid.

2. Petioles 2 cm. long or more; fruiting pedicels 4 cm. long or more, the calyx-lobes deciduous from the massive receptacle ..... **Astrocasia**

2. Petioles, and usually fruiting pedicels, much shorter.

3. Leaves only 1–2 mm. long ..... **Andrachne**

3. Leaves larger.

4. Branches glabrous.

5. Fruit not separating regularly into cocci; seed-coat fleshy without, bony within, the hilum deeply excavated **Margaritaria**

5. Fruit regularly dehiscent into 3 cocci; seed coat neither fleshy nor bony, the hilum not excavated.

6. Seed bullate-rugose, the hilum abaxial ..... **Chascotheca**

6. Seed otherwise.

7. Leaves coriaceous and narrowly spathulate, or else branches ending in spines ..... **Securinega**

7. Leaves otherwise; branches never spiny.

8. Herbs or subshrubs, or if shrubby (*P. botryanthus*) then fruits borne on "naked" thyrses ... **Phyllanthus**

8. Trees; fruit axillary to foliage leaves ..... **Savia**

4. Branches pubescent.

5. Branches hirtellous with spreading hairs ..... **Phyllanthus**

5. Branches sericeous-pilose with appressed hairs ..... **Savia**

Once a doubtful specimen has been assigned to *Phyllanthus*, the task of determining it to species may still appear rather formidable. The first step should always be to decide whether or not the branching is phyllanthoid (cf. Jour. Arnold Arb. 37: 104 et seq. 1956). Since the sex and number of flowers produced per node is often an important character, it should be kept in mind that this can often be determined even from a branch that has lost most of its flowers; the number of pairs of persistent bracteoles usually give a good indication of the number of flowers, and the stumps or scars of the female flower pedicels are usually distinctly larger in diameter than those of males.

Flower-parts should be measured in water at a magnification of 15 to 50 diameters if exact correspondence with the descriptions is desired. How-

ever, in practice measurements taken from dried organs on the herbarium specimen are often accurate enough. It should be kept in mind, however, that the measurements apply in most cases to fully mature organs. Since some structures, particularly staminal and stylar columns, may undergo great elongation at anthesis, due allowance must be made for measurements taken from the bud.

The height of the staminal column, when there is more than a single whorl of anthers, is measured from the base to the attachment of the upper whorl of anthers. The length and breadth of the anthers are given in relation to their morphologically longitudinal axes. As discussed in the section on floral morphology, the direction of dehiscence of the anther is expressed topographically, i.e., in relation to the long axis of the entire flower rather than of the individual stamen.

Because of the diverse stylar configurations in the genus, it is difficult to express the dimensions in consistent terms. If the styles are erect and united, the height of the stylar column is given. If they are free and spreading, the length given in the descriptions refers to the purely topographical extent to which they can be straightened out when moistened. The degree of division of the style, on the other hand, refers to its total length and takes into account any twists which cannot be uncoiled.

The size, shape, and ornamentation of the seeds furnish excellent characters for purposes of identification. The stated dimensions are understood to apply in relation to the longitudinal (vertical) axis of the seed as it sits in the capsule. Thus the radial dimension is measured along either of the lateral faces or on the flat face if one of them is carinate, while the tangential is the width of the seed when lying on its back. Since the capsules of many species tend to dehisce — even if immature — when the specimen is dried, immature seeds may often be found mixed with the mature ones. This makes it difficult to determine the actual range in seed size, particularly since in some species the two seeds of a locule are normally unequal in size. Usually, however, one can distinguish well-developed seeds by their plumpness, more well-defined ornamentation, and less shiny surface.

The specimens cited in this work have been made available through the courtesy of the curators of the following institutions [1]: Arnold Arboretum (A); Botanisches Museum, Berlin-Dahlem (B); British Museum (Natural History), London (BM); Jardin botanique de l'Etat, Brussels (BR); Botanical Museum and Herbarium, Copenhagen (C); Chicago Natural History Museum (F); Conservatoire et Jardin botaniques, Geneva (G); Gray Herbarium (GH); Systematisch-Geobotanisches Institut, Universität Goettingen (GOET); Science Museum, Institute of Jamaica, Kingston (JAM); Herbarium, Royal Botanic Gardens, Kew (K); Rijksherbarium, Leyden (L); Herbario de la Salle, Vedado, Habana (LS); University Herbarium, University of Michigan, Ann Arbor (MICH); Missouri Botanical Garden, St. Louis (MO); Herbier Marie-Victorin, Institut

[1] Herbarium abbreviations are the standard ones of Lanjouw and Stafleu, Index Herbariorum ed. 2 (1954), except for the Science Museum, Institute of Jamaica, which is unlisted.

Botanique, Université de Montreal (MT); New York Botanical Gardens (NY); Museum National d'Histoire Naturelle, Laboratoire de Phanérogamie, Paris (P); Naturhistoriska Riksmuseum, Stockholm (S); Herbarium, Estación Agronómica de Cuba, Santiago de las Vegas, Habana (including Herbarium of Juan Roig) (SV); Herbarium, Imperial College of Agriculture, Port of Spain (TRIN); United States National Museum, Department of Botany, Washington (US); Naturhistorisches Museum, Vienna (W).

Phyllanthus L. Sp. Pl. 981. 1753.
Niruri Adans. Fam. Pl. **2:** 356. 1763.
Urinaria Medic. Malvenfam. 80. 1787.
Diasperus O. Ktze. Rev. Gen. **2:** 596. 1891.

Trees, shrubs, or herbs of very diverse habit. Branching either unspecialized — the phyllotaxy spiral or distichous — , or phyllanthoid, i.e., the spiralled leaves on main axes reduced to cataphylls which subtend deciduous branchlets with distichous leaves. Leaves varying greatly in size and texture but always entire, and glabrous in most species; petiole always much shorter than the blade; stipules deciduous or persistent, often indurate. Plants monoecious or subdioecious, rarely dioecious; inflorescences axillary (sometimes pseudoterminal), or more or less greatly reduced cymes, these aggregated into thyrses in some species; the individual flowers bibracteolate. Flowers apetalous; calyx gamophyllous, 4–6-lobed, the lobes imbricate in the bud (decussate in calyces with 4 lobes); disk nearly always present in the flowers of both sexes. Male flower pedicellate; stamens 2–15, mostly 3–6; filaments free or connate; anthers free or connate, almost invariably extrorse; disk usually divided into segments alternating with the calyx-lobes, less commonly undivided; pistillode absent; pollen grains oblong to globose, with various ornamentation patterns, small (c. 15–35 μ in diameter). Female flower pedicellate or subsessile; calyx-lobes 5 or 6 (rarely 4), entire or less commonly toothed or lacerate; disk various: cupuliform or plane, entire or lobed or divided into segments, absent in a few species; staminodia absent (except in *P. acidus*); ovary usually of 3 carpels, in a few species of 4 up to 12 (only 2 in *P. chacoensis*), smooth or less commonly roughened, bullate, or hairy; ovules always two in each locule, usually collateral (at least at first), anatropous or amphitropous, with two integuments; nucellus usually projecting beyond exostome as a beak in contact with the obturator; embryo-sac the normal 8-nucleate type; styles erect or spreading, free or united into a column, bifid, multifid, or dilated into an entire or lacerate stigma. Fruit mostly a dehiscent capsule (the cocci explosively dehiscent in many species), less commonly baccate or drupaceous, the carpels normally separating as crustaceous cocci from a persistent columella. Seeds usually two in each locule, sometimes unequal, rarely only one developing to maturity; seed-coat dry, crustaceous, smooth or variously ornamented; endosperm whitish, cartilaginous; embryo straight or slightly curved, the cotyledons usually considerably broader than the radicle.

TYPE SPECIES: *Phyllanthus niruri* L.

As delimited in this work, *Phyllanthus* is primarily an Old World genus, only about 200 of the 650 species being native to the New World. The West Indian region, however, harbors a disproportionately high percentage of the native American species; in the western hemisphere only southern Brazil appears to be a comparably important center of speciation.

A detailed analysis of the generic relationships of *Phyllanthus* is beyond the scope of the present treatment. Here it must suffice to say that of the other West Indian genera of Phyllantheae, a close affinity is shown only by *Margaritaria*, which is well distinguished by its very different fruit structure. Still more closely related but evidently generically distinct are a series of Old World genera with phyllanthoid branching: *Glochidion*, *Breynia*, *Sauropus*, and *Phyllanthodendron*.

The generic limits of *Phyllanthus*, as here interpreted, correspond rather closely to those earlier held by Pax (Natürl. Pflanzenfam. ed. 1, 3(5): 18–23. 1890), with the exception that *Margaritaria* is here recognized as a distinct genus. The subgeneric divisions, on the other hand, are very different from those in the interpretations of Mueller and of Pax. The most radical innovations are the grouping of the sections into subgenera and the breaking up of the Muellerian sect. *Euphyllanthus* into a number of small sections, some of which belong to different subgenera. These changes in concept, which are now undertaken only after study of representatives of all sections of the genus (whether West Indian or not), are due largely to the application of new criteria — in particular, the branching and pollen types. Since, however, examination of the small pollen grains of *Phyllanthus* is very inconvenient for making routine identifications, the reader may prefer to use the artificial key to the subgeneric groups (Appendix I).

SYNOPSIS OF THE SUBGENERA[2]

1. Branching not phyllanthoid; herbs or subshrubs with spiral or distichous leaves; stamens 3, filaments (in ours) free; pollen grains (in ours) colporate. . . . . I. **Isocladus**

1. Branching phyllanthoid, or if not then plants shrubby and filaments connate.
   2. Pollen grains colporate, striate, or foveolate;[3] woody or herbaceous, branching phyllanthoid; stamens 2–5, filaments free or connate; fruit various.
      3. Stamens 5; pollen grains colporate; carpels 3–10 . . . . . II. **Kirganelia**[4]
      3. Stamens 2–4.
         4. Trees with drupaceous or pithy fruits; carpels 3 or 4; pollen grains colporate . . . . . III. **Cicca**[5]
         4. Herbs or low shrubs with capsular fruits; carpels 3; pollen grains colporate, striate, or foveolate . . . . . IV. **Phyllanthus**

[2] The keys and descriptions are in most cases based solely on West Indian material, and do not take into account exceptional species outside our limits.

[3] Apparently acolpate in an anomalous species of subg. *Phyllanthus*.

[4] Subgenus **Kirganelia** (Juss.), stat. nov. *Kirganelia* Juss. Gen. Pl. 387. 1789.

[5] Subgenus **Cicca** (L.), stat. nov. *Cicca* L. Mant. 17. 1767.

2. Pollen grains otherwise; entirely woody; stamens 2–15, filaments usually connate; fruit capsular, dry or rarely somewhat fleshy.
   3. Pollen grains porate; perianth segments lacerate; stamens 2 ..... V. **Eriococcus**
   3. Pollen grains not porate; perianth segments not lacerate.
      4. Pollen grains echinulose, with short colpi; stamens 3; branching phyllanthoid, branchlets bipinnatiform VI. **Conami** [6]
      4. Pollen grains areolate.
         5. Branching not phyllanthoid; stamens 3 VII. **Botryanthus** [7]
         5. Branching phyllanthoid; stamens 2–15 .... VIII. **Xylophylla**

Subgenus I. **Isocladus,** subg. nov.[8]

Herbs or shrubs with unspecialized branching, the leaves spirally or distichously arranged. Monoecious or dioecious. Male flower: calyx-lobes 5; disk-segments 5; stamens 3, the filaments free or united, anthers dehiscing vertically or horizontally; pollen grains colporate or areolate with ora midway between the angles. Female flower: calyx-lobes 5; disk cupuliform or of 5 segments, the segments often bifid; ovary 3-celled, styles free or united. Fruit a dehiscent capsule; seeds trigonous, smooth or verruculose.

This subgenus is typified by sect. *Paraphyllanthus*,[9] which does not occur in the West Indies; our representatives all belong to sect. *Loxopodium*. Subgenus *Isocladus* includes the species which vegetatively appear to be the least specialized within the genus. The species of sect. *Paraphyllanthus*, in particular, are similar in aspect to some species of *Andrachne*; but the male flower is so different in the two groups that a direct relationship appears unlikely.

In addition to sects. *Paraphyllanthus* and *Loxopodium*, subg. *Isocladus* also includes sects. *Macraea* and *Anisolobium*, these last being primarily Old World groups. The subgenus as a whole is thus circumtropical in distribution and comprises about 60 species of diverse habit.

[6] Subgenus **Conami** (Aubl.), stat. nov. *Conami* Aubl. Hist. Pl. Guian. Fr. 926–927, *pl. 354.* 1775.

[7] Subgenus **Botryanthus, subg. nov.** Frutices vel arbores monoicae ramulis distichis, glabris vel hirsutulis, foliis nonnihil magnis; floribus axillaribus vel in thyrsis; flore masculo laciniis calycis plerumque 6, staminibus 3, filamentis connatis, antheris plusminusve horizontaliter dehiscentibus, granis pollinis globosis, areolatis; flore femineo laciiniis calycis 6, disco integro vel crenato, ovario loculis 3, stylis erectis, connatis, ad apicem reflexis; capsula sicca, seminibus laevibus. — Species typica *Phyllanthus grandifolius* L.

[8] Subgenus **Isocladus,** subg. nov. Herbae fruticesve, ramificatione disticha vel spirale; flore masculo staminibus 3, filamentis liberis vel connatis, granis, pollinis oblongis vel globosis, sulcatis vel areolatis; flore femineo disco integro vel dissecto, ovario laeve loculis 3, stylis bifidis; capsula in coccis 3 dehiscentia; seminibus trigonis verruculosis vel laevibus — Species typica *Phyllanthus maderaspatensis* L.

[9] The type of sect. *Paraphyllanthus* (Muell. Arg. Linnaea **32:** 3. 1863; DC. Prodr. **15**(2): 355. 1866) is hereby designated as *P. maderaspatensis* L.; and the section is redefined so as to exclude all species with phyllanthoid branching, such as *P. urinaria* L.

Sect. 1. **Loxopodium** Webster, Contr. Gray Herb. 176: 46. 1955.

Geminaria Raf. Western Minerva 42. 1821.
Synexemia Raf. Neogenyton 2. 1825.

Annual or perennial herbs, sometimes suffruticose; primary axis or axes erect, bearing distichous leaves and axillary flowers; branches terete, compressed, or winged. Stipules acuminate, more or less auriculate or appearing peltate at the base, entire or denticulate. Leaf-blade membranous or chartaceous, not over 3 cm. long.

Monoecious, subdioecious, or dioecious, the flowers present on all orders of branching in contracted unisexual or bisexual cymes. Male flower: pedicel slender, articulate near the middle; calyx-lobes 5 or 6; disk of 5 or 6 distinct segments; stamens 3, filaments free or rarely connate at base; anthers subglobose or flattened, the connective enlarged adaxially; anther-sacs opening horizontally; pollen grains oblong, 4-colporate, the ora transversely elongate, reticulation obscure. Female flower: pedicel straight at anthesis, becoming geniculate-reflexed in fruit, usually 1 mm. long or less; calyx-lobes 5 or 6; disk cupuliform, lobed, or parted into 5 or 6 segments; ovary smooth; styles free or somewhat fused basally, usually bifid. Capsule green or reddish, not strongly nerved; seeds trigonous, brown to fuscous, not over c. 1.7 mm. long, verruculose or smooth.

TYPE SPECIES: *P. caroliniensis* Walt.

This strictly New World group of perhaps a half dozen species (and a number of subspecies) is well defined by the completely distichous phyllotaxy, flowers on all orders of branching, and colporate pollen grains. Some of the species of the Old World sect. *Macraea* are very similar to the West Indian plants both in aspect and in floral morphology, but they have very different areolate pollen grains. A very close similarity in many details is also shown by the species of sect. *Urinaria*, which however have phyllanthoid branching. Members of sect. *Loxopodium* are as a rule small and inconspicuous plants; they tend to be mesophytes growing in wet savannas and along stream-beds, but some varieties of *P. caroliniensis* are found on dry limestone areas.

KEY TO THE SPECIES

1. Capsule 2 mm. or less in diameter, the seed 0.7–1 mm. long; stem and branches terete or flattened, not winged; strictly monoecious, the cymules bisexual. . . . . 1. *P. caroliniensis*
1. Capsule about 3 mm. in diameter, the seed 1.3–1.7 mm. long; stems and branches flattened, sharply angled or winged; male and female flowers at separate axils.
   2. Seed smooth; capsule olivaceous; annual with subsimple stems; styles appressed, horizontal. . . . . 2. *P. hyssopifolioides*
   2. Seed verruculose; capsule reddish; perennial with stems clustered on a caudex; styles erect-ascending. . . . . 3. *P. heliotropus*

1. **Phyllanthus caroliniensis** Walt. Fl. Car. 228. 1788.

Diasperus carolinensis (Walt.) O. Ktze. Rev. Gen. 2: 598. 1891.

Annual or short-lived perennial herbs, usually erect, mostly 1–3 dm. high, the base never becoming more than softly woody; taproot usually simple, with filiform lateral roots. Primary stem straight with pinnately arranged branches (branches of tertiary order sometimes developing), or replaced above by few to several erect secondary branches. Branches terete or somewhat flattened, never winged (in West Indian forms), greenish, brownish, or reddish-tinged, smooth or papillate-scabridulous, the internodes quite variable in length (2–15 mm.). Stipules ovate-triangular to lanceolate, acute or more often acuminate, usually more or less auriculate at the base, nearly entire to conspicuously dentate, thin and papery or becoming slightly toughened, pale brown or reddish-brown, 0.7–2 mm. long, 0.4–0.6 mm. broad. Petioles smooth, 0.5–1 mm. long. Leaf-blades obovate, elliptic, or oblong, obtuse or rounded and apiculate (rarely sharply acute), acute at the base, c. 5–20 mm. long, 2–10 mm. broad, membranous to rather firm; above bright green or olivaceous, usually smooth, the nerves only slightly raised; beneath green, pruinose, or rubescent, smooth to papillate, midrib prominently raised, lateral veins often somewhat raised, tertiary veinlets anastomosing to form a delicate reticulum, or not visible; margin scarcely to conspicuously thickened, smooth or scabridulous.

Monoecious, all axils except the lowest on the primary stem normally floriferous; cymules axillary, greatly reduced: male flowers 1 or 2, followed by 1 or 2 (rarely 3) female flowers.

Male flower: pedicel c. 0.6–1 mm. long. Calyx-lobes (5) 6, oblong to suborbicular, rounded or obtuse, more or less entire, 0.5–0.7 mm. long, 0.5–0.8 mm. broad, thin and scarious, pale yellowish (rarely pink-tinged), 1-nerved. Disk of (5) 6 elliptic to broadly cuneate entire or crenulate segments. Stamens 3, filaments free, obliquely ascending; anthers emarginate, anther-sacs parallel, inserted on the adaxially broadened connective, opening horizontally, not confluent.

Female flower: pedicel sharply reflexed, usually geniculate, smooth, terete, often reddish-tinged, 1 mm. long or shorter. Calyx-lobes 6 (rarely 5 or 7), linear-oblanceolate to oblong, rounded to acute, 0.6–1.4 mm. long, with a narrow to broad whitish or yellowish often reddish margin and a thicker convex herbaceous midrib area, red-tinged at the base or sometimes entirely reddish, 1-nerved, the midrib plane without, saliently raised within. Disk entire or lobed or dissected into roundish or cuneate segments, rather thin, not glandular. Ovary smooth; styles free and sharply ascending or somewhat fused at the base and more or less horizontally spreading, not over c. 0.3 mm. long, bifid (sometimes shallowly so), the arms slender or thickened, spreading apart or recurved, rounded or subcapitate at the tip.

Capsule c. 1.6–2 mm. in diameter when mature but often precociously dehiscent; valves thin, smooth, olivaceous or reddish-tinged, nervation obscure. Seeds 0.7–1 mm. long, 0.6–0.75 mm. radially and tangentially,

usually dull greyish-brown when mature, verruculose, i.e., covered with evenly or rather irregularly spaced dark raised points.

This is the most widespread and — with the possible exception of *P. niruri* — most variable of the New World species of *Phyllanthus*. It occurs from Illinois and Pennsylvania south throughout most of tropical America to Argentina and Paraguay, although in parts of this range it may be an introduced weed, and has also colonized the Galapagos Islands. Its true limits have not been understood owing to the rather confused treatment by Mueller Argoviensis in the "Prodromus" (1866), where the different populations are distributed among no less than four different species: *P. pruinosus*, *P. schomburgkianus*, *P. caroliniensis*, and *P. stenopterus*, these last two placed considerably distant from the first two. Although the systematic elaboration of *P. caroliniensis* will itself require a special monograph, it is already evident that the species includes some distinctive subordinate taxa with well-defined ranges. In the West Indies these are three:

KEY TO THE WEST INDIAN SUBSPECIES

1. Branches scabridulous with papillae scattered or in striae; disk of female flower lobed or parted into segments; calyx-lobes of female flower broadly oblong or spathulate, usually rounded or obtuse, often reddish-tinged to the tip, 0.6–0.9 (–1) mm. long; styles appressed; leaves firm, the tertiary veinlets usually very obscure or invisible. . . . . ssp. *saxicola* (1c)
1. Branches quite smooth; disk of female flower entire or obscurely angled; calyx-lobes of female flower narrower, more acute, usually not red-tinged except at base; styles more or less ascending; leaves thinner, margin scarcely thickened, tertiary veinlets usually forming an evident reticulum beneath.
   2. Stipules 0.8–1.2 mm. long; disk-segments of male flower cuneate-squarish or roundish, as broad as or broader than long; leaves obovate, tapering from above middle to base; calyx-lobes of female flower mostly linear-spathulate, (0.9) 1–1.2 (–1.4) mm. long . . . . ssp. *caroliniensis* (1a)
   2. Stipules 1.5–2 mm. long; disk-segments of male flower ovate or elliptic, mostly longer than broad; leaves more often elliptic, tapering at or below middle toward base; calyx-lobes of female flower oblong or spathulate, mostly 0.7–0.9 mm. long . . . . . ssp. *guianensis* (1b)

Another subspecies from Panama, Colombia, and perhaps other parts of South America may eventually be found in the West Indies. It is distinguished at once by its narrowly winged stems and is here designated as **Phyllanthus caroliniensis** ssp. **stenopterus** (Muell. Arg.) comb. nov. (*P. stenopterus* Muell. Arg. Prodr. **15**[*2*]: 399. 1866).

1a. **Phyllanthus caroliniensis** ssp. **caroliniensis**.

(PLATE XIII, *figs. A, B*).

Phyllanthus caroliniensis Walt. Fl. Car. 228. 1788.

Phyllanthus obovatus Muhl. ex Willd. Sp. Pl. **4**: 574. 1805.

Geminaria obovata Raf. First Cat. Bot. Gard. Transylv. Univ. 14. 1824.

Synexemia caroliniana Raf. Neogenyton 2. 1825.

Synexemia obovata Raf. ibid.
Synexemia pumila Raf. ibid.
Synexemia cuneifolia Raf. New Fl. N. Amer. **4:** 100. 1838.
Euphorbia ludoviciana Featherman, Bot. Surv. So. & Centr. La. 71. 1871.
Andrachne pumila (Raf.) House, Bull. N. Y. State Mus. **233–234:** 66. 1921.
Phyllanthus graminicola Britton, Bull. Torr. Bot. Club **48:** 333. 1922.

Erect annual herb 1–3 dm. high, primary stem with several to many lateral branches; branches smooth or furrowed, not scabridulous; stipules triangular-lanceolate, denticulate especially toward the base, thin and scarious, (0.8–) 1–1.2 mm. long, 0.5–0.6 mm. broad. Leaves obovate or elliptic, rounded and apiculate or obtuse at the tip, 6–13 mm. long, 4–7 mm. broad, smooth on both sides and margins; midrib above plane, beneath conspicuously raised (at least proximally), the laterals (4 or 5 on a side) forming with the tertiaries a delicate reticulum. Male flowers solitary, each associated with 2 or 3 females in the cymule, calyx-lobes 6, segments of the disk cuneate or squarish, as broad as or broader than long. Female flower: calyx-lobes 6, linear-lanceolate or narrowly spathulate, acute, green, (0.9–) 1–1.2 (–1.4) mm. long, 0.2–0.3 mm. broad; disk cupular, enclosing ⅓ to ½ the ovary at anthesis, entire. Capsule c. 1.7 mm. in diameter, green; seeds light greyish brown, 0.8 mm. long, 0.65 mm. radially (in West Indian specimens).

TYPE: Herb. Thomas Walter, sheet 83 (holotype in BM not seen, but photograph in GH library examined).

DISTRIBUTION: more or less coextensive with the range of the species (MAP I).

JAMAICA: St. Mary: Castleton grounds, alt. 500 ft., *Harris 12143* (F, GH, JAM, MO, US).

LESSER ANTILLES: SWAN ISLANDS: Eastern Swan Is., 17.22° N., growing in sand, *Lord Moyne 4* (NY). MARTINIQUE: *Bélanger 222* (P), *293* (G, P), *670* (P), *782* (P); *Duss 48* (ex p., mixed with ssp. *guianensis*, F, NY); cultures, Balata, *Mouret 113* (P). TOBAGO: The Widow, near Easterfield, on banks of the main road, *Broadway 3515* (F). TRINIDAD: hb. Hooker (P); Woodbrook, wild in garden, *Broadway 6675* (S); coastal plain, grassy roadside, Carenage, *Britton & Hazen 12* (NY, HOLOTYPE of *P. graminicola*; GH, US, ISOTYPES); swale, O'Meara Savanna, *N. L. & E. G. Britton 2502* (GH, TRIN).

The West Indian specimens of ssp. *caroliniensis* represent heterogeneous and sporadic populations; the specimens at least from Jamaica and Martinique have probably been introduced. The Trinidad form, made a separate species *P. graminicola* by Britton, has very narrow calyx lobes and small seeds but represents at most a rather unimportant variant of ssp. *caroliniensis*.

1b. **Phyllanthus caroliniensis** ssp. **guianensis** (Klotzsch) Webster [10] var. **antillanus** Muell. Arg. Linnaea **32:** 36. 1863.

[10] Contr. Gray Herb. **176:** 46. 1955.

Phyllanthus schomburgkianus β *antillanus* Muell. Arg. in DC. Prodr. **15**(2): 387. 1866.

Erect sparsely branched herb becoming 2–4.5 dm. high; branches smooth, often quite flattened above. Stipules rather narrowly triangular-lanceolate, acuminate, denticulate or entire, mostly 1.5–2 mm. long, c. 0.5–0.6 mm. broad. Leaf-blades elliptic to oblong or obovate, often broadest at or slightly below the middle, 8–22 mm. long, 4–10 mm. broad, smooth on both sides and on margins, thin, the reticulum of tertiary veinlets visible beneath. Male flowers paired (sometimes single?); calyx-lobes 6, disk-segments ovate or elliptic, definitely longer than broad, obscurely glandular at the tip. Female flowers 1 or 2 per axil; calyx-lobes 6, oblong to spathulate, acute or obtuse, green or reddish-tinged only at the base, 0.7–0.9 (–1) mm. long, (0.2–) 0.25–0.4 (–0.5) mm. broad; disk entire or roundly angled; styles free, ascending. Capsule c. 1.7–2 mm. in diameter; seed 0.9–1 mm. long, 0.75–0.8 mm. broad.

TYPE: Martinique, *Sieber Herb. Martin. Suppl. 10.*

DISTRIBUTION: var. *antillanus* is endemic to the Lesser Antilles (MAP I).

LESSER ANTILLES. ANTIGUA: *Wüllschlagel 496, 497* (GOET); Fig Tree Hill, a weed in the S.W. (volcanic) district, *Box 1226* (F, US). MONTSERRAT: weed in provision lands, alt. 1200 ft., *Shafer 178* (NY, US). GUADELOUPE: 1839, *Beaupertuis* (P); dans les champs cultivés, Camp Jacob, *Duss 2447b* (F, NY, US); *Quentin 254* (P). DOMINICA: woodlands on the western slopes of Morne Brule, Portsmouth, *Hodge 573A* (NY); Montpelier, *Lloyd 582* (NY). MARTINIQUE: 1858, *Bélanger 220* (P); 1867–70, *Hahn* (P); herb. Vaillant (P); S. Marie, *Bordas 7* (P); abondant le long des routes, Fonds St. Denis, Camp-Balata, &c., *Duss 48* (ex p., mixed with ssp. *caroliniensis*, F, NY, US); Herb. Martin. Suppl. 10, *Sieber* (L, W, SYNTYPES).

This plant is the Antillean representative of the South American ssp. *guianensis*, agreeing with var. *guianensis* in the stipules and male flowers and hardly differing in anything more than leaf shape. On Martinique var. *antillanus* occurs together with ssp. *caroliniensis*, which has presumably been introduced; there is no evidence that intergradation has occurred, but no careful field studies have been made. By virtue of its large stipules and elliptic disk segments in the male flower, ssp. *guianensis* is a very well-characterized group; but when the entire range of variation of *P. caroliniensis* is taken into account, it does not appear to warrant the rank of a separate species.

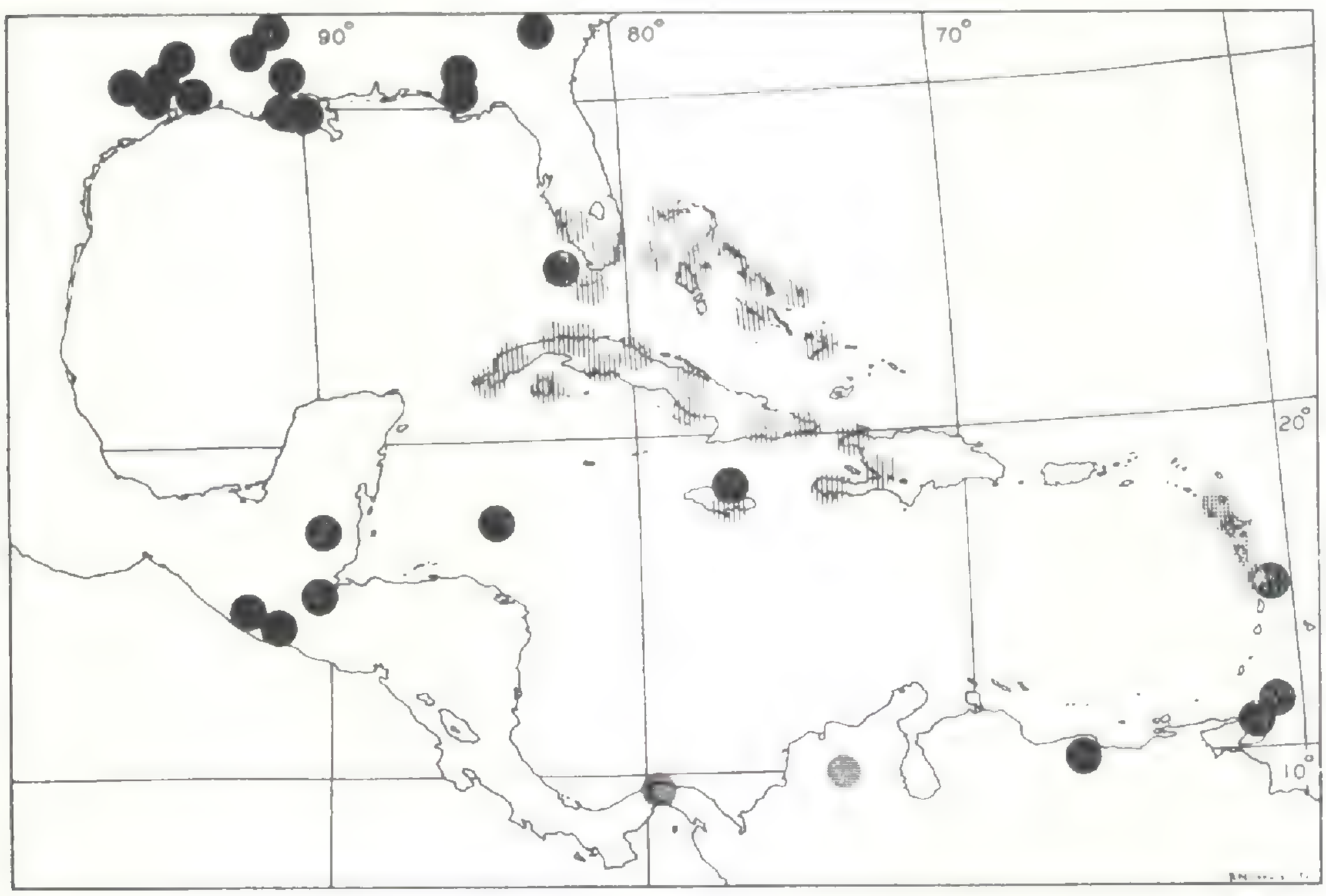
1c. **Phyllanthus caroliniensis** ssp. **saxicola** (Small) Webster, Contr. Gray Herb. **176**: 46. 1955. (PLATE XIII, *figs. C, D*).

Phyllanthus saxicola Small, Bull. N. Y. Bot. Gard. **3**: 428. 1905.

Phyllanthus pruinosus sensu Muell. Arg. in DC. Prodr. **15**(2): 387. 1866. Not *P. pruinosus* Rich. in Sagra, Hist. Nat. Cuba **11**: 216. 1850.

Erect annual or short-lived perennial, the primary stem either bearing pinnately arranged secondary branches or with few to several erect secondary branches clustered near its top; branches with minute papillae

either in discontinuous striae or densely arranged. Stipules triangular, acuminate, obscurely to conspicuously denticulate, (0.7–) 1–1.2 (–1.5) mm. long, 0.4–0.6 mm. broad. Leaf-blades narrowly elliptic to obovate, acute or more commonly obtuse or rounded-apiculate at the tip, acute at the base, 5–12 (–18) mm. long, 2–8 mm. broad, usually rather firm, bright green to olivaceous above, green to pallid beneath, secondary veins obscure above, usually evident and often raised beneath, tertiary veinlets ordinarily very obscure or quite invisible. Male flowers 1 or 2 per axil; calyx-lobes 6, olivaceous or infrequently reddish-tinged, c. 0.6–0.7 mm. long; disk-segments squarish or cuneate, about as broad as long. Female flowers 1 or 2 per axil; calyx-lobes 6 (rarely 5 or 7), mostly oblong to rather broadly spathulate and rounded to subacute at the tip, 0.6–0.9 (–1) mm. long, (0.2–) 0.3–0.5 (–0.6) mm. broad, green with pink-tinged scarious margins or often brilliantly red-stained, rarely lacking reddish color; disk usually lobed to irregularly or regularly divided into 6 cuneate or spathulate segments; styles more or less horizontally spreading. Capsule (1.5–) 1.6–1.75



MAP I. Distribution of the Caribbean representatives of *Phyllanthus caroliniensis* Walt.: black dots, ssp. *caroliniensis*; vertical lines, ssp. *saxicola*; stippling, ssp. *guianensis* (var. *antillanus*); fine horizontal lines, ssp. *stenopterus*.

(–1.9) mm. in diameter, green or red-stained. Seeds (0.7–) 0.75–0.9 mm. long, 0.6–0.75 mm. radially and tangentially, dark-fuscous or light greyish brown.

TYPE: Florida, Dade County, everglades between Cocoanut Grove and Cutler, November 1903, *Small & Carter 775* (NY, HOLOTYPE).

DISTRIBUTION: southern Florida to Greater Antilles (MAP I).

BAHAMAS: GREAT BAHAMA: rocky clearing, Eight Mile Rocks, *Britton & Millspaugh 2489* (F, NY); palmetto lands, Barnett's Point, *Britton & Millspaugh 2623* (GH, MO, NY, US). BIMINI: open sandy field, North Bimini, *R. A. & E. S. Howard 10014* (US). BERRY ISLANDS: Great Stirrup Cay, on limestone, *Britton & Millspaugh 2273* (F, NY); Great Harbor Cay, sandy soil, *Britton & Millspaugh 2333* (F, NY); Little Harbor Cay, cultivated ground, *Britton & Millspaugh 2250* (F, NY, US). ANDROS: northern section, coppice near Fresh Creek, *Small & Carter 8799* (F, GH, NY, US); Long Bay Cays, *Brace 5021* (F, NY); Kemp Bay, *Brace 5026* (F, NY). NEW PROVIDENCE: near Nassau, *Curtiss 79* (F, G, GH, L, M, MICH, MO, NY, P, US); Tea House, *E. G. Britton 3447* (NY); Hog Island, moist sandy places, *P. Wilson 8263, 8344* (F, MO, NY). ELEUTHERA: Governor's Harbor and vicinity, low meadow, *Britton & Millspaugh 5514 ex p.* (F); Glass Window to Harbor Island, thickets, *Britton & Millspaugh 5394* (F, NY); Harbor Island to the Bluff, *E. G. Britton 6504* (F, NY). EXUMA: Great Guana Cay, *Britton & Millspaugh 2861* (GH, NY, US). CAT ISLAND: Orange Creek and vicinity, white lands near Cotton Point, *Britton & Millspaugh 5746* (F, NY); the Bight and vicinity, moist ground, *Britton & Millspaugh 5928* (F, NY); Little San Salvador, red lands, *Britton & Millspaugh 5698* (F, NY). WATLING'S ISLAND: Cockburn Town, *P. Wilson 7207* (F, GH, NY), *Britton & Millspaugh 6076* (F, NY); southwest end, *P. Wilson 7337* (F, GH, MO, NY). ACKLIN'S ISLAND: Gold Rock, *Brace 4376* (F, NY).

CUBA: Without definite locality, *Poeppig* (P); *Wright 590* (BR, F, G, GH GOET, MO, NY, P, S, US), *591* (S). PINAR DEL RIO: Las Martinas to the coast, *Shafer 11095* (NY, US); banks of San Diego River not far from San Diego de los Baños, *León & Hioram 4519* (NY), *León 4411, 4553* (NY), *Roig 2330* (SV). ISLA DE PINOS: *Blain 174* (F); Caleta Cocodrilos, coastal limestone, *Britton, Wilson, & León 15293* (F, GH, MO, NY, US). HABANA: cerca de Rincón, *Wilson 1055* (NY); coastal sands between Río Cojimar and Playa de Bacuranao, *P. Wilson 9529* (NY); valley of Cuente Blanca River near Guanabacoa, *León 500* (NY); banks of Quibú River, Marianao, *León 3674* (NY, SV); inter Campo Florido et Loma de Coca, *Ekman 1242* (S). MATANZAS: along railroad near Ibarra, *Britton, Britton, & Shafer 340* (NY); prope Matanzas, *Rugel 292* (NY); in graminos humides in pratis salsis ad Matanzas, *Poeppig* (BR, MO, P, W). LAS VILLAS: Ciénaga de Zapata, montes, Santo Tomas, *Acuña 4333* (SV); a orillas rio Caibarién, *Fernando 482* (NY). CAMAGÜEY: savanna north of La Gloria, in grass, *Shafer 360* (NY, US); Santa Cruz del Sur ad Río Najassa, *Ekman 8612* (S). ORIENTE: Bayate, border of Río Cauto, *Ekman 1964, 2442* (S); Sierra Maestra, *León 10748* (NY); Sevilla Estate near Santiago, upper Guama River, alt. 550 ft., *N. Taylor 164* (NY); steep banks of the Río Jojo c. 7 km. north of Cajovavo, *Webster 4000* (MICH); stony banks of Jauco River, Jauco, *León 11686* (NY); gorge of the Río Yamurí, in sandy crevices of rock near the river, *Shafer 7853* (NY); vicinity of Baracoa, in yard, *Shafer 3906* (NY); playa de Mata, Baracoa, *Acuña & Diaz Barreto 18615* (SV); Baracoa, between Yumurí and Mata, on shady limestone rock, *Ekman 3646* (S).

JAMAICA: ST. CATHERINE: Spanish Town, in damp hollows, *Harris 12046* (C, F, GH, JAM, MO, NY, P, S, US).

HAITI: NORD-OUEST: rocky bed of Môle Road, west bank of Riv. Côte de Fer, *E. C. & G. M. Leonard 12751* (US); vicinity of Jean Rabel, dry bed of Môle road on west bank of Riv. Côte de Fer, *E. C. & G. M. Leonard 13687* (NY, US); vicinity of Port à L'Ecu, bare mountain slope facing sea, west of bay, *E. C. & G. M. Leonard 13879* (GH, K, MO, NY, US); Presqu'île, Port-de-

Paix, limestone terraces west of Saline-Michel, quite rare, *Ekman H3948* (S). OUEST: arid coastal thicket west of Cabaret, *E. C. & G. M. Leonard 11838* (GH, K, MO, NY, US). SUD: Massif de la Hotte, western group, Pestel, Dalcour, laterite soil, c. 400 m., *Ekman H9011* (S, US).

DOMINICAN REPUBLIC: Barrabas [province not indicated], *Raunkiaer 784* (C).

This subspecies of southern Florida, the Bahamas, and the Greater Antilles is perplexingly variable and eventually may be divided into several varieties. It grows in a wide variety of habitats including pinelands on limestone, salty meadows, sandy wastes, abandoned fields, etc., with perhaps an overall preference for rocky, shaded streambeds. The plants from southern Florida (at the type locality) and from Great Bahama Cay comprise a geographic race which differs from most of the rest of the subspecies by virtue of darker seeds, red-tinged male flowers, and more depauperate habit. These characters can scarcely be defined well enough for purposes of identification, however. Moreover, since there are in Cuba and Haiti a number of aberrant types, it does not seem practicable to describe outlying segments of the main population as varieties. Some collections, particularly those from Haiti, have scarcely scabridulous stems (even with close inspection under a lens!) and are thus hardly separable from ssp. *caroliniensis*.

2. **Phyllanthus hyssopifolioides** HBK. Nov. Gen. & Sp. 2: 108. 1817. (PLATE XIII, *figs. E–G*).

Phyllanthus hyssopifolius Muell. Arg. in DC. Prodr. **15**(2): 390. 1866, sphalm.
Diasperus hyssopifolius ("HBK.") O. Ktze. Rev. Gen. **2**: 599. 1891.
Phyllanthus monocladus Urb. Repert. Sp. Nov. **15**: 404–405. 1919.

Erect annual herb, completely smooth and glabrous; main stem unbranched or with very few laterals, 1–2.5 dm. high, 0.5–1 mm. in diameter, light brown, below terete, above becoming flattened and with a thin narrow wing c. 0.1–0.15 mm. broad at the margins; internodes 5–9 mm. long. Leaves: stipules ovate-lanceolate, acuminate, auriculate, more or less denticulate, midrib area as in *P. heliotropus*, 1.2–1.5 mm. long, 0.6–0.7 mm. broad. Petioles 0.5–0.8 mm. long, plano-convex, adaxially grooved. Leaf-blades ovate, oblong, or elliptic, obtuse-apiculate at the tip, obtuse to rounded at the base, 6–12 mm. long, 2.5–5 mm. broad; above olivaceous, beneath pallid, green, or dull reddish; midrib raised above and beneath, laterals 4 or 5 on a side, obscure but usually visible above, beneath visible or obsolete; margin smooth.

Monoecious (sometimes dioecious?), the male and female flowers at separate axils, the male in few-flowered clusters (sometimes apparently solitary at branch-tips), the female solitary; male and female flowers irregularly alternating, with occasional axils barren.

Male flower: pedicel c. 0.5 mm. long. Calyx-lobes 5, obovate to orbicular or broader than long, rounded, entire, 0.6–0.7 mm. long, 0.6–0.9 mm. broad, scarious-hyaline, pale yellowish, the midrib unbranched, no herbace-

ous midstrip developed. Disk-segments 5, cuneate to orbicular, inconspicuously crenulate, rather thin, not evidently glandular, c. 0.2 mm. in diameter. Stamens 3, filaments free, c. 0.15 mm. long, obliquely ascending; anthers subglobose, 0.25–0.3 mm. broad, the slits confluent.

Female flower: pedicel 1 mm. long or less, geniculate. Calyx-lobes 6, oblong to obovate-oblong, obtuse or subacute, (0.8–) 1–1.2 mm. long, 0.4–0.7 mm. broad. Disk of 6 cuneate entire segments. Ovary smooth; styles horizontal, bifid, the greatly dilated and thickened branches spreading and appressed on the top of the ovary, less than 0.2 mm. long.

Capsule subglobose, c. 1.9 mm. high and 3 mm. broad, olivaceous, not veined. Seed bluntly trigonous, 1.6–1.7 mm. long, 1.4–1.5 mm. radially and tangentially, dull chestnut-brown with a thin easily rubbed-off yellowish coating, quite smooth, the ornamentation due to the outlines of the wavy rows of longitudinally elongated cells; hilum circular, purplish-black.

TYPE: Venezuela, Orinoco region, Santa Barbara, Maypure, *Humboldt* (Herb. Humboldt, P).

DISTRIBUTION: savannas, Hispaniola and northern South America (MAP 11).

DOMINICAN REPUBLIC. DUARTE: Cordillera Septentrional, Matanzas, Sabana del Pinal, not common, *Ekman H15878* (S). TRUJILLO: savannah land and lake area between Bayaguana and Guerra, *R. A. & E. S. Howard 9934* (US). SEIBO: Cordillera Central, Sabana de la Mar, in savannas, not common, *Ekman H15612* (S; this locality originally in Prov. Samaná).

TRINIDAD: Piarco Savanna, *Crueger* (GH), *Baker* (TRIN 14854); O'Meara Savanna, *Britton & Hazen 1573* (TRIN), *Broadway* (TRIN 9341).

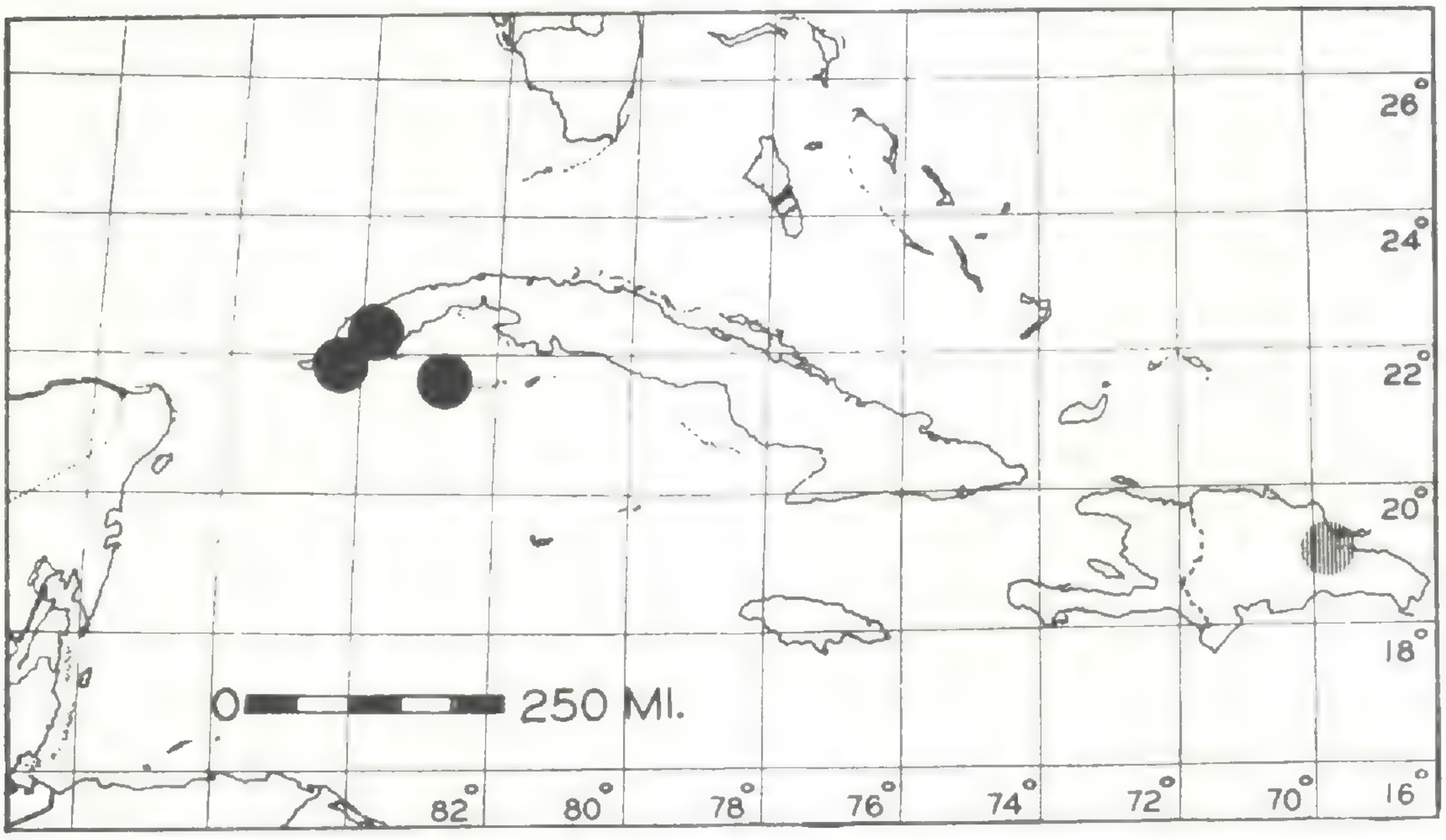
The identification of the specimens from Hispaniola as this characteristically South American species is one of the more surprising phytogeographic discoveries made during this study. The material collected by Ekman and the Howards matches Mueller's description in the "Prodromus" (1866: 390) in all essential details. The very characteristic seeds, present in the mature condition in both Ekman collections, establish the identity of the Hispaniolan plant beyond doubt. The type specimen in Humboldt's herbarium in Paris differs from the West Indian plants in the small capsule (c. 2.5 mm. in diameter) and calyx-lobes only 0.7–0.8 mm. long, but nevertheless appears clearly to be conspecific.

Although *Broadway 2130* from Piarco Savanna, Trinidad — the type collection of *P. monocladus* Urb. — has not been examined, the Crueger specimen from the same locality surely represents the same population. The Trinidad plants differ from the Hispaniolan ones only in their somewhat smaller size, while they correspond in all the technical characters. *Phyllanthus monocladus* may therefore be relegated to synonymy with confidence.

3. **Phyllanthus heliotropus** Wright ex Griseb. Goett. Nachr. **1865**: 167. 1865; emend. Muell. Arg. in DC. Prodr. **15**(2): 388. 1866. (PLATE XIV).

Diasperus heliotropus ("Gris. em.") O. Ktze. Rev. Gen. **2:** 599. 1891.

Erect perennial (but flowering the first year), entirely smooth and glabrous, the primary axis becoming a thickened, dark-brown caudex up to 1–2 cm. long and 5 mm. thick, with few to many somewhat thick subsimple or branched dark brown lateral roots. Stems clustered atop the caudex, unbranched or with one or very few laterals, becoming mostly 3–5 (–7) dm. high, c. 1–1.5 mm. thick, greenish brown to deep chestnut



Map II. Distribution of *Phyllanthus heliotropus* Wright ex Griseb. (black dots) and *P. hyssopifolioides* HBK. (lined dots) in the Greater Antilles.

brown, more or less terete at the very base but above soon flattened and with a narrow sharp wing 0.1–0.2 mm. wide, or merely acute-angled near ends of branches; internodes variable, decreasing in length from c. 7–15 mm. at base of large stems to c. 3–5 mm. at tips and on smaller stems. Stipules ovate-lanceolate, acuminate, auriculate, obscurely to conspicuously dentate, the midvein of the thickened dark basal median area extending as a conspicuous rib through the light to dark brown scarious margins, (1–) 1.3–1.7 (–2) mm. long, 0.5–0.9 mm. broad. Leaves: petioles plano-convex, grooved above, 0.7–1 mm. long, dark brown. Blades mostly oblong or sometimes ovate or elliptic, obtuse and mucronate at the tip, obtuse or rounded at the base, those on main stems mostly 5–12 mm. long and 2.5–6 mm. broad (somewhat smaller at tips and on smaller branches), subcoriaceous, bright to dull olivaceous above, olivaceous to reddish-bronzen or silvery beneath, the midrib depressed but visible above, salient and running to the mucro beneath; margin thickened, smooth or with irregular thickenings.

Dioecious or subdioecious (rarely monoecious), sporadic female flowers occasionally appearing on otherwise male plants, the female and male flowers always at different axils; female flowers solitary (rarely paired);

male flowers in densely bracteolate monochasia eventually becoming 1–2 mm. long (but appearing as if in clusters of 2 or 3 at tips of branches or on plants flowering the first year).

Male flower: pedicel slender, 0.6–0.8 mm. long above the articulation. Calyx-lobes 5 or 6, oblong to obovate or suborbicular, rounded-obtuse to subtruncate, entire, (0.6–) 0.7–0.8 (–1) mm. long, 0.6–0.9 (–1) mm. broad, the yellowish scarious margins broader than the narrow to obsolete greenish midstrip; midrib unbranched, running to the tip. Disk-segments 5 or 6, orbicular to cuneate, 0.25–0.35 mm. long, entire or obscurely wavy, not evidently glandular. Stamens 3, completely free (very rarely united halfway), 0.3–0.5 mm. long, obliquely ascending; anthers swollen adaxially at the top of the filament (thus appearing globose from behind), 0.2–0.25 mm. long, 0.25–0.4 mm. broad; anther-sacs discrete, opening horizontally and transversely.

Female flower: pedicel geniculate, becoming c. 1 mm. long, reddish. Calyx reddish-tinged, massive at the base; calyx-lobes 5 or 6, ovate to oblong in flower, oblong to oblong-ovate in fruit, rounded or obtuse, entire, (0.9–) 1–1.3 mm. long, (0.5–) 0.6 0.75 (–0.9) mm. broad, spreading or reflexed, midstrip dark green but usually deeply reddish-stained, scarious margins broad; midrib plane without, salient within. Disk cut to the base into 5 or 6 squarish or cuneate more or less emarginate segments c. 0.35–0.4 mm. in diameter, these yellowish, rather thick, smooth and nearly entire, not evidently glandular. Ovary smooth, deeply sulcate; styles free, erect-ascending, c. ⅓–fid, c. 0.35 mm. long, 0.2 mm. wide across the thick and fleshy divaricate and recurved branches.

Capsule depressed-globose, c. 1.7 mm. high, (2.7–) 2.8–3 mm. broad, deep lavender-reddish, no nervation visible on sides. Seeds trigonous, (1.3–) 1.35–1.55 mm. long, (1–) 1.2–1.3 (–1.4) mm. radially, 1–1.3 mm. tangentially, chestnut-brown to fuscous, lucid becoming dull, with scattered raised black points; hilum dark purplish-brown, triangular or roundish.

TYPE: Cuba, Pinar del Rio, *Wright 1945* (GOET, HOLOTYPE; F, G, GH, NY, P, S, US, ISOTYPES). The collection in the Gray Herbarium has in a packet manuscript notes by Wright indicating the localities as: "savannas, Vueltabajo", and "Pinales Hatequemado". "Vueltabajo", however, is merely a general name for a large stretch of tobacco-growing country in Pinar del Rio; and the Pinales Hatequemado have not been identified.

DISTRIBUTION: endemic to Cuba and the Isle of Pines (MAP II).

CUBA: PINAR DEL RIO: *Wright 1945* (GOET, HOLOTYPE; F, G, GH, NY, P, S, US, ISOTYPES); Laguna Santa María, wet sand, *Britton, Britton, & Gager 7184* (NY); Laguna Jovero, dry sand, *Shafer 10708* (F, NY, US); Laguna Los Indios and vicinity, in water, *Shafer 10804* (NY); between Guane and Remates, sabanas near El Payuco, *Killip 32363* (GH, US); savanes de San Luis, *Marie-Victorin & Alain 326, 354* (MT); Laguna Redonda, between Pinar del Río City and La Coloma, fairly common in white sand, *Webster 4672* (GH, MICH); between Pinar del Río and Coloma, Colpothrinax savanna, *Britton et al. 6608*

(F, NY); Herradura, in sandy pinelands, *Ekman 10735* (S). Isla de Pinos: Santa Barbara, Colpothrinax savanna south of railroad, *Earle* (NY); Nueva Gerona, edge of cultivation, *Curtiss* (NY); Prendio Modelo, Nueva Gerona, sabanas, *Roig 8806* (SV); Columbia, in low moist sandy pinelands, edge of a pond, *Ekman 12396* (S); vicinity of Los Indios, white sand, *Britton, Britton, & Wilson 14174* (F, NY, US).

This plant, characteristic of savannas and pinelands of western Cuba, takes its specific epithet from Wright's manuscript notes that the plant "spreads its leaves to the morning sun". It is related on the one hand to *P. pudens* Wheeler of Texas, but also to *P. hyssopifolioides*. In seed characters it agrees with the former but in the male flower and in fruit size it approaches more closely to the latter. It is also related to the widespread *P. compressus* which, however, is monoecious and has monadelphous stamens. These species, together with a few others of South America, comprise a complex whose distribution pattern parallels that of the subspecies of *P. caroliniensis*; but in this case the differentiation between the groups is so pronounced that they certainly represent distinct species.

(*To be continued*)

EXPLANATION OF PLATES

PLATE XIII

Figs. A–B. *Phyllanthus caroliniensis* ssp. *caroliniensis* (*Harris 12143* [GH]): A. branch, × 4; B. female flower, × 10.

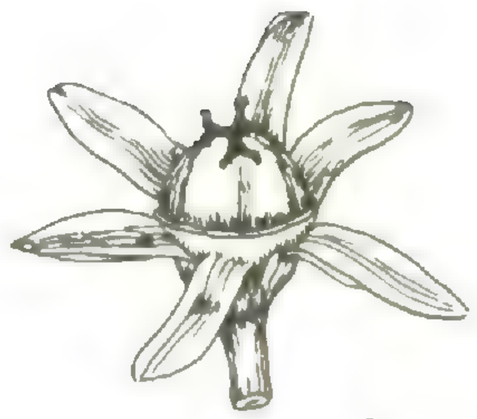
Figs. C–D. *Phyllanthus caroliniensis* ssp. *saxicola* (*Small & Carter 8799* [GH]): C. female flower, × 10; D. branch, × 4.

Figs. E–G. *Phyllanthus hyssopifolioides* (*Baker 14854* [TRIN]): E. branch, × 4; F. female flower, × 10; G. fruiting calyx, × 10.

PLATE XIV

Phyllanthus heliotropus Wright ex Griseb. (*Killip 32363* [GH], figs. A–B, D–E; *Webster 4672* [GH], fig. C): A. habit, c. ½ natural size; B. branch, × 5; C. male flower, × 20; D. female flower, after fertilization, × 10; E. seed, × 8.

A



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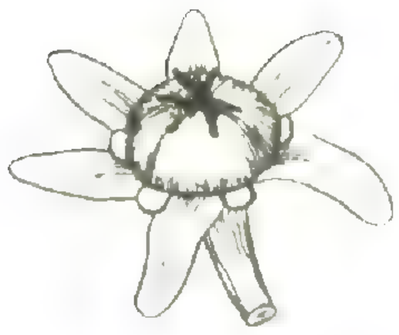
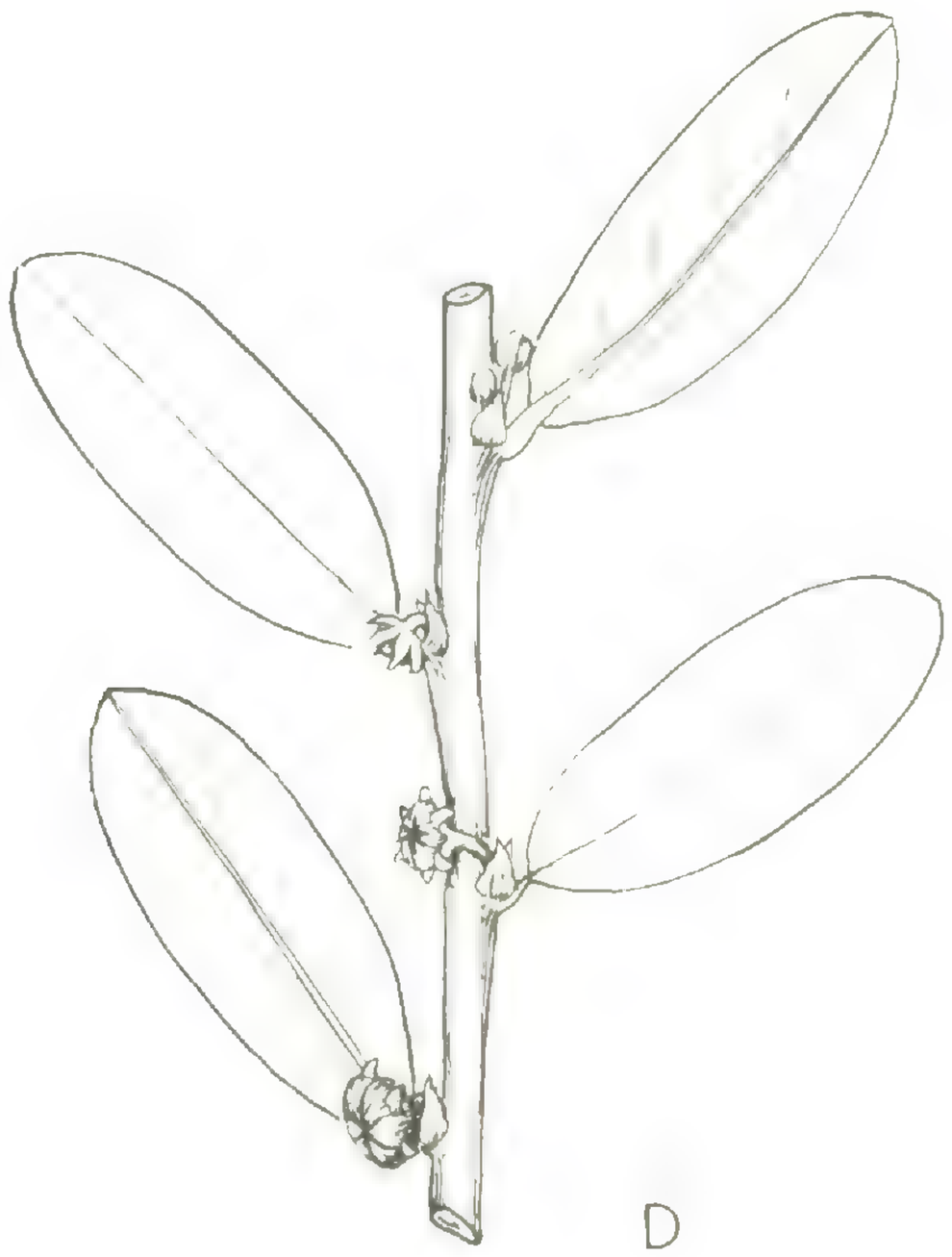


C



D

E

F

G

D. Hall

WEBSTER, WEST INDIAN PHYLLANTHUS

WEBSTER, WEST INDIAN PHYLLANTHUS

THE RELATIONSHIP BETWEEN SPHENOSTEMON OF NEW CALEDONIA AND NOUHUYSIA OF NEW GUINEA

I. W. Bailey

In reducing the genus *Nouhuysia* to *Sphenostemon* — as a basis for emphasizing a closer relationship between the floras of New Guinea and New Caledonia — Van Steenis (7) concluded his brief paper with the statement, "it is still desirable that the wood anatomy be examined." Having published with Dr. Swamy (1) a detailed study of the endomorphic structures of *Nouhuysia* and of the congeneric *Idenburgia* I proceeded to assemble material of the three known species of *Sphenostemon* for a comparative investigation. In so doing, I was unaware of the fact that Dr. Metcalfe had undertaken, at the suggestion of Professor Erdtman, a study of the anatomy of the stems and leaves of *Sphenostemon*. Doctor Metcalfe has kindly sent me an advance copy of his manuscript. Since I am in complete agreement with his descriptions and conclusions, I shall not attempt to record in detail my own observations upon the anatomy of the vegetative organs of *Sphenostemon*, but shall confine my attention primarily to the reproductive ones.

A totality of available evidence from leaves and small stems of herbarium specimens is clearly indicative of close relationship between *Sphenostemon* and *Nouhuysia*. Particularly significant are similarities in the occurrence and distribution of styloids, in nodal anatomy (trilacunar), in vasculature of the leaf (characteristic more or less triangular stele in the petiole and midrib of the lamina), and in the primitive structure of the first-formed secondary xylem. However, as concluded by Metcalfe (6) available anatomical evidence is insufficient for determining whether the genera are congeneric. In this connection, it is desirable to obtain material from the outer parts of large stems as such material frequently exhibits a wider range of structural differences than do the first-formed secondary tissues of small twigs.

MATERIAL

My investigation of the reproductive structures of *Sphenostemon* is based upon material obtained from the following herbarium specimens: *Sphenostemon balansae* Baill. (*Balansa 1330*), flowers, pollen. *Sphenostemon comptonii* Baker (*Compton 1693*), flowers, pollen. *Sphenostemon pachycladum* Baill. (*Buchholz 1297*), flowers, pollen, fruits; (*Franc* in Herb. Arnold Arb.), flowers, pollen.

The extensive collections of *Idenburgia* and *Nouhuysia* utilized for comparative purposes are listed in the paper by Bailey and Swamy (1).

POLLEN

In commenting upon *Sphenostemon* at the VIII[th] International Botanical Congress, Erdtman (4) suggested that "it might be worth while to investigate whether or not the similarity between the strange pollen grains in this genus and those in *Idenburgia* (or *Nouhuysia*), another genus of uncertain taxonomic position from New Guinea, is taxonomically significant." His suggestion appears to have been based upon a comparison between the pollen of *Sphenostemon balansae* Baill. (*Balansa 1330*) and that of *Nouhuysia papuana* Laut. (*Kostermans 2198*).

When examined in water or lactic acid, the pollen grains of the three species of *Sphenostemon* are closely similar in size ($\pm$ 10 $\times$ 13 μ), in form (oblate) and in structure (3-porate and conspicuously reticulate at magnifications of 600–1500). The pores or apertures in the nexine are relatively large for grains of such comparatively small size and are circular or oval, the orientation of the latter varying from lolongate to lalongate. The polar sexine, as noted by Erdtman (5), is at times thinner with faint or absent reticulation. Each pore is subtended by a plug of colorless, transparent, hygroscopic material which expands when moistened, bulging the tenuous sexinous covering outward. This hyaline substance removes ruthenium red very rapidly from dilute solutions in advance of the gradual deeper staining of the protoplast. In this respect, it resembles the papillae which project from moistened pollen of the New World species of *Drimys*, Bailey and Nast (2).

As previously shown by Bailey and Swamy (1), the pollen of *Nouhuysia* varies markedly in size, form, and structure. The large ($\pm$ 35 μ), spherical, nonaperturate grains of *Brass 12661* and *Clemens 5499b* have a conspicuously thickened nexine. The tenuous sexine has a faintly detectable pitted or granular appearance at high magnification. The pollen of other collections of *Nouhuysia* differs in being smaller, oblate and provided with conspicuous pores of varying size, number and orientation. The grains of *Clemens 2422* are 4-porate with an admixture of 5-porate ones, those of *Rutten 2240* are 4-porate with an admixture of 3-porate grains and those of *Kostermans 2217*, *Kostermans 2198*, and *Gibbs 5654* are 3-porate with an admixture of 4-porate ones. The transparent material, which subtends the pores, varies in amount and in the case of the relatively small apertures of more or less circular form in *Kostermans 2217*, *Clemens 2422* and *Rutten 2240* is only slightly protuberant when the pollen is moistened, in contrast to the conspicuous protrusions that occur through the larger, oval, usually lolongate pores of *Kostermans 2198* and *Gibbs 5654*. The pollen from *Kostermans 2217* and *Clemens 2422* have a clearly visible reticulate sexine, but of finer texture than that of *Sphenostemon*. This is in contrast to the sexine of *Clemens 3828*, *Kostermans 2198*, *Gibbs 5654* and *Rutten 2240* which has a faintly visible sculpture at high magnification, thus resembling that of the nonaperturate pollen of *Brass 12661* and *Clemens 5499b*.

Although the pollen from each collection of *Nouhuysia* differs from that

of *Sphenostemon* in one or more of its morphological characters, there is a combination of diagnostic criteria in the genus as a whole which, as noted by Erdtman (4), is strongly suggestive of relationship between *Nouhuysia* and *Sphenostemon*. However, evidence from pollen *by itself* is at present inadequate for determining whether the two categories of plants are congeneric.

STAMENS

The stamens of the three species of *Sphenostemon*, as in the case of the stamens of *Degeneria*, *Himantandra* and a number of other ranalian (sensu lato) genera, cannot be described adequately in conventional terms of filament, anther and connective. They are relatively broad,[1] fleshy micro-

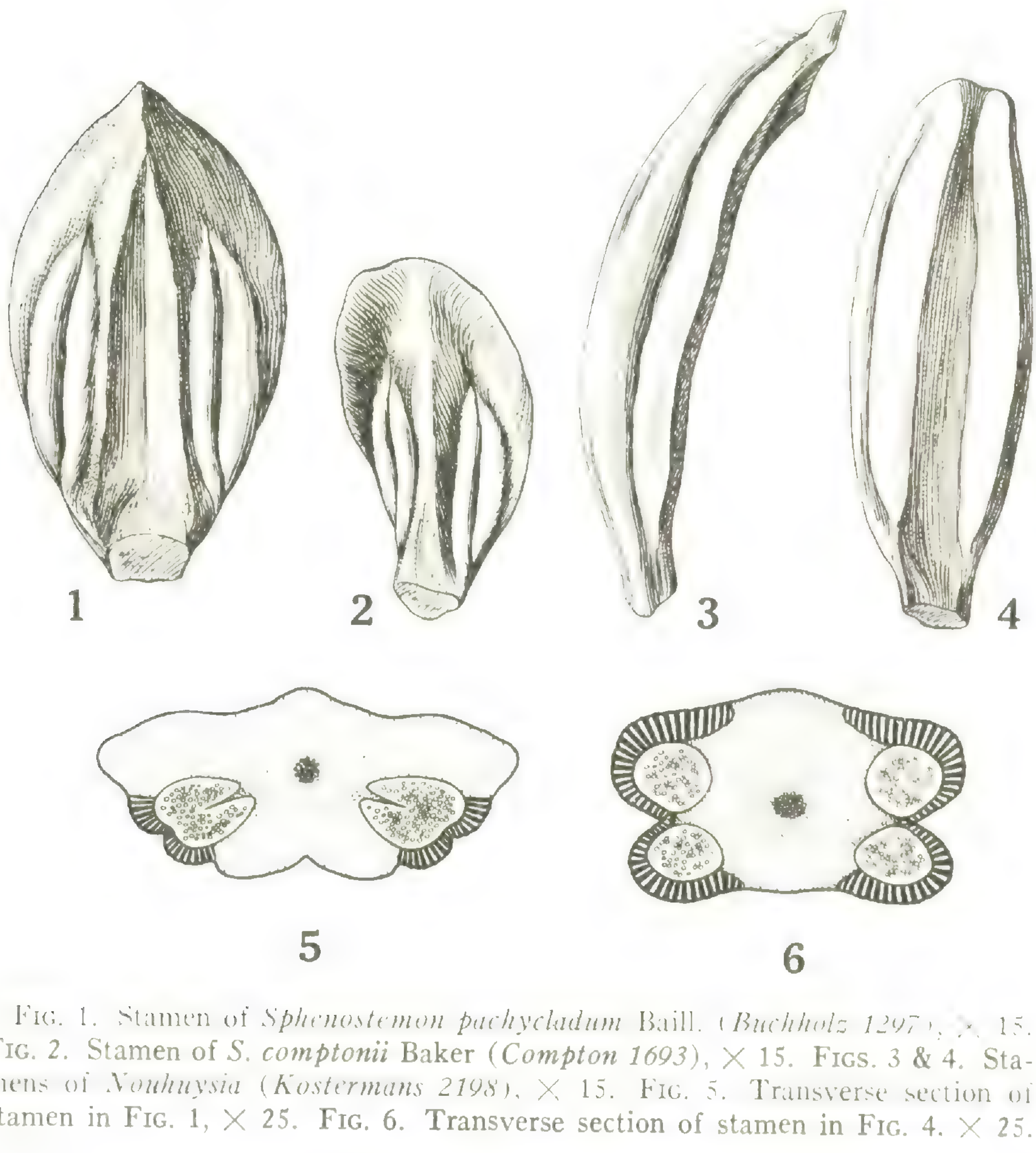


FIG. 1. Stamen of *Sphenostemon pachycladum* Baill. (*Buchholz 1297*), × 15. FIG. 2. Stamen of *S. comptonii* Baker (*Compton 1693*), × 15. FIGS. 3 & 4. Stamens of *Nouhuysia* (*Kostermans 2198*), × 15. FIG. 5. Transverse section of stamen in FIG. 1, × 25. FIG. 6. Transverse section of stamen in FIG. 4. × 25.

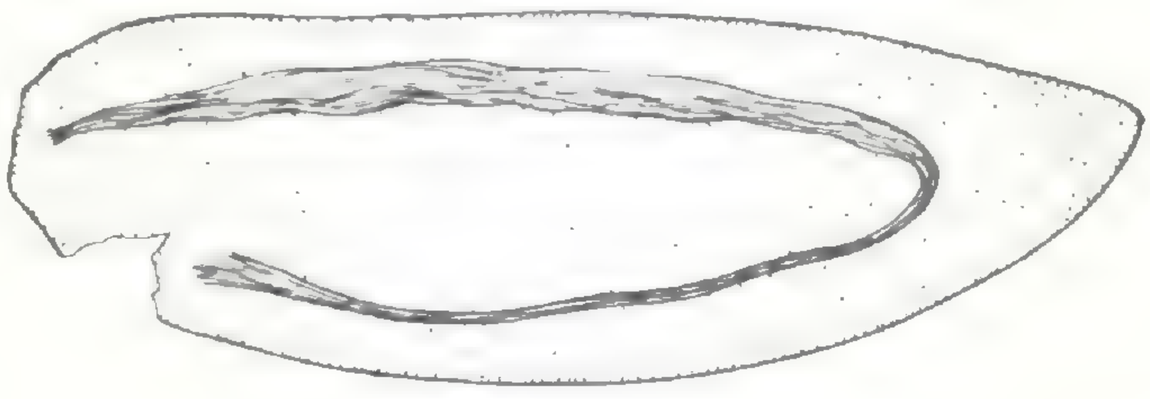
[1] It should be noted in this connection that the normal form of the stamens, i. e. where they are able to expand symmetrically, is frequently modified by excessive lateral pressures of expanding, closely congested organs in the flower buds

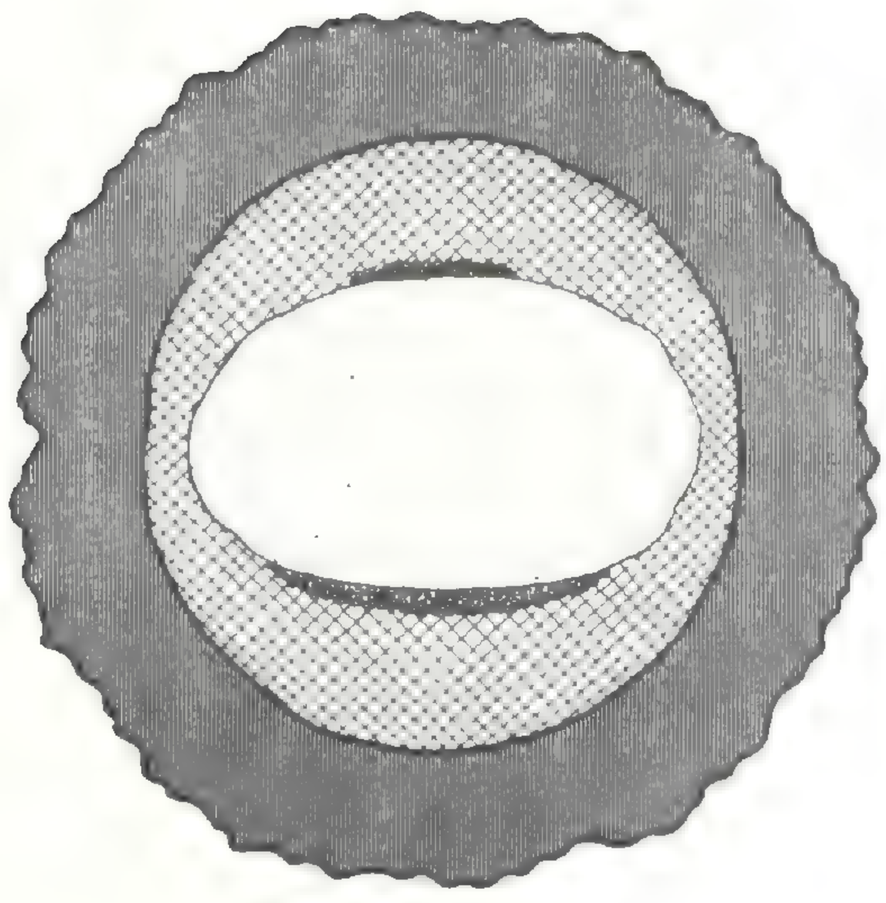
sporophylls, *Figs. 1 & 2*, having deeply embedded sporangia, *Fig. 5*. As in the case of *Degeneria* and *Himantandra*, the fibrous parts of the hypodermis ("endothecium") are restricted to limited areas confronting the sporangia, *Fig. 5*.

In contrast, the stamens of *Nouhuysia* resemble sessile conventional anthers with extensive, markedly protuberant sporangia, *Figs. 3, 4 & 6*. The fibrous parts of the hypodermis are more extensive, *Fig. 6*, in certain collections, e. g. *Clemens 2422*, jacketing the exposed surfaces of the "connective" as well as confronting the protuberant parts of the sporangia.

SEEDS

The seeds of all investigated collections of *Nouhuysia*, and of the congeneric *Idenburgia*, are characterized by a centripetally, deeply lobed stony layer with a corresponding conspicuously ruminate nutritive layer, *Fig. 9*. The vascular system consists of a number of strands, or branches from the supply at the base of the seed. In *Fig. 9*, there are seven such strands, each corresponding with one of the major ruminations of the nutritive layer. The embryo is rudimentary and minute.





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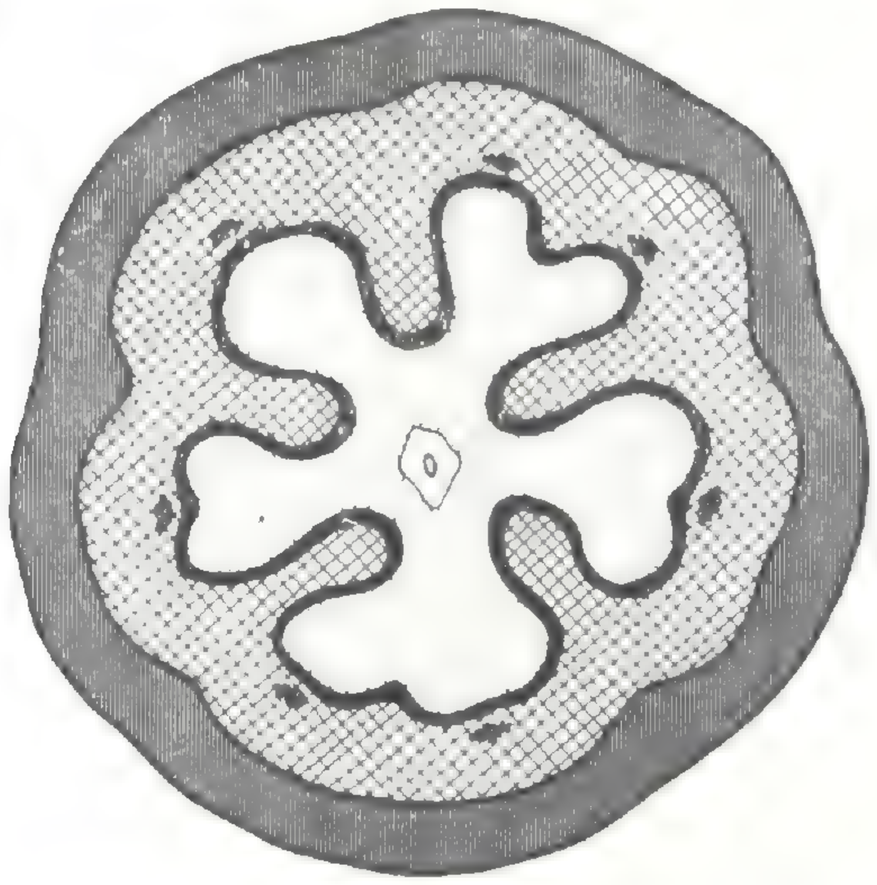

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FIG. 7. Cleared seed of *S. pachycladum* Baill. (*Buchholz 1297*), showing pattern of vasculature, × 5. FIG. 8. Transverse section of fruit and seed of *S. pachycladum* Baill. (*Buchholz 1297*), × 10. FIG. 9. Transverse section of fruit and seed of *Nouhuysia* (*Clemens 2240*), × 9; carpellary wall dark, stony layer cross-hatched, nutritive layer stippled, vascular strands dark.

The dry fruits of *Sphenostemon pachycladum* Baill., *Buchholz 1257*, are of much elongated form (22 × 6 mm.) in contrast to the more or less globose (12 × 10 mm.) or subglobose (15 × 12 mm.) fruits of *Nouhuysia*. The correspondingly elongated seeds contract markedly in drying, but even when reexpanded the sclerotesta and nutritive layers exhibit no evidence of lobing or rumination, *Fig. 8*. The vascular tissue is in the form of a *single* broad band which extends from the base of the seed toward the apex and back again toward the level of attachment of the seed, *Figs. 7 & 8*. That the absence of rumination is not due to immaturity of the fruit is indicated by the fact that rumination of the undifferentiated tissues of *Nouhuysia* is detectable during early stages of the enlargement of the seeds.

DISCUSSION

Evidence from all organs is clearly indicative of close relationship between *Sphenostemon* and *Nouhuysia*. The most conspicuous differences between the two categories of plants are in the reproductive, rather than in the vegetative, organs. The problem of the congeneric status of the genera resolves itself, accordingly, into a matter of consistency in taxonomic judgments. Does the totality of morphological differences exceed the limits of a single generic boundary?

The most outstanding and consistent differences between available collections from New Caledonia and those from New Guinea are at present in the stamens. However, if the seeds of *S. comptonii* Baker and *S. balansae* Baill. resemble those of *S. pachycladum* Baill., fundamental differences in vasculature and rumination may eventually prove to be equally, if not more, significant taxonomically.

It should be noted in this connection that broad microsporophylls with more or less deeply embedded sporangia occur in various representatives of the Magnoliaceae, as well as in *Degeneria* and *Himantandra*. As demonstrated by Canright (3) the chief specializations in the stamens of the Magnoliaceae (sensu stricto) appear to be (1) elongation of the apices, (2) differentiation of a filament, (3) reduction in the number of veins from three to one, (4) an increase in the relative size of the sporangia and a concomitant increase in their amount of protuberance, (5) transition from a laminal to a marginal position of the sporangia, and (6) development of an enveloping fibrous layer in the "connective." It is evident that the differences between the stamens of *Sphenostemon* and those of *Nouhuysia* involve changes comparable to items 4–6 in the Magnoliaceae. If broad sessile microsporophylls with deeply embedded sporangia, e. g. *Magnolia maingayi* King, are to be retained in the genus *Magnolia*, it might not be inconsistent taxonomically to reduce *Nouhuysia* to *Sphenostemon*. However, it seems that final judgment in such matters should be based upon the totality of evidence from all parts of the plant rather than upon similarities or differences in any single organ or morphological feature.

When the differences in the stamens are considered in connection with differences in the pollen, in the seeds, and in the perianth (*Nouhuysia*, 4

tepals or "sepals"?, *Sphenostemon*, 8 tepals or 4 "sepals"? + 4 "petals"?) it appears premature to reduce *Nouhuysia* to *Sphenostemon* until additional material of the plants has been collected and carefully investigated. Furthermore, striking differences in the pollen from different collections of *Nouhuysia* raises the question whether all of them can be included in *N. papuana* Laut.

It should be emphasized in conclusion that the microsporophylls of *Sphenostemon* and the very primitive structure of the xylem in both *Nouhuysia* and *Sphenostemon* make these genera unusually significant phylogenetically. They clearly do not belong in the Guttiferae or Trimeniaceae and it seems unlikely that they are closely related to the Aquifoliaceae. More comprehensive investigations of adequately preserved material are essential for determining their true relationships.

ACKNOWLEDGMENTS

I am much indebted to Dr. George Taylor of the British Museum for his courtesy in sending material of *Sphenostemon comptonii* Baker, to Professor G. Neville Jones for specimens of *S. pachycladum* Baill. collected by Buchholz, and to the Paris Museum of Natural History for the loan of various collections of *Sphenostemon*.

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THE CONDUPLICATE CARPEL OF CANANGA ODORATA

K. PERIASAMY AND B. G. L. SWAMY

RECENT INVESTIGATIONS by Prof. I. W. Bailey and his colleagues on the representatives of the ranalean families have brought to light several features of great morphological value. Among the more important of these is the concept of the "conduplicate carpel," first put forward by Bailey and Smith (1942), Bailey and Nast (1943), and further elaborated by Bailey and Swamy (1951).

The concept of the conduplicate carpel was primarily the outcome of an effort to understand and interpret the remarkable megasporophyll of the Degeneriaceae, a new family recently added to the Ranales (Bailey and Smith, 1942). According to Bailey and Smith, "The carpel of *Degeneria*, preceding and during anthesis, resembles an adaxially folded 3-veined sporophyll. . . . Furthermore, the margins of the carpel are not infolded or coherent during ontogeny, but tend to flare apart externally. The placentation is clearly laminar and adaxial." This remarkable nature of the carpel of *Degeneria* instigated further investigations, and Bailey and Nast (1943) found that not only carpels of a fundamentally similar type occur in the representatives of the Winteraceae, but that this family as a whole exhibits also various trends of phylogenetic modifications of such primitive ranalean megasporophylls. As a result of their investigations on the Degeneriaceae and Winteraceae, Bailey and Nast (1943) concluded that the carpels of these families "do not conform with the classical interpretation of the angiosperm carpel as an involute megasporophyll bearing marginally attached ovules." Following this, Bailey and Swamy (1951) have given a clear and coherent picture of the course of carpel evolution in the Ranales. They have shown that, proceeding from the least modified form of surviving carpel exhibited by *Drimys piperita*, the various other morphological forms may be derived as logical consequences of certain simple trends of modification.

Although the evidences presented in the contributions cited above are sufficient to warrant a modification of the "classical" view of the carpel which comprehends the megasporophyll of angiosperms as an involute structure with marginal placentation, it is desirable to present further evidence which would strengthen the "conduplicate" view.

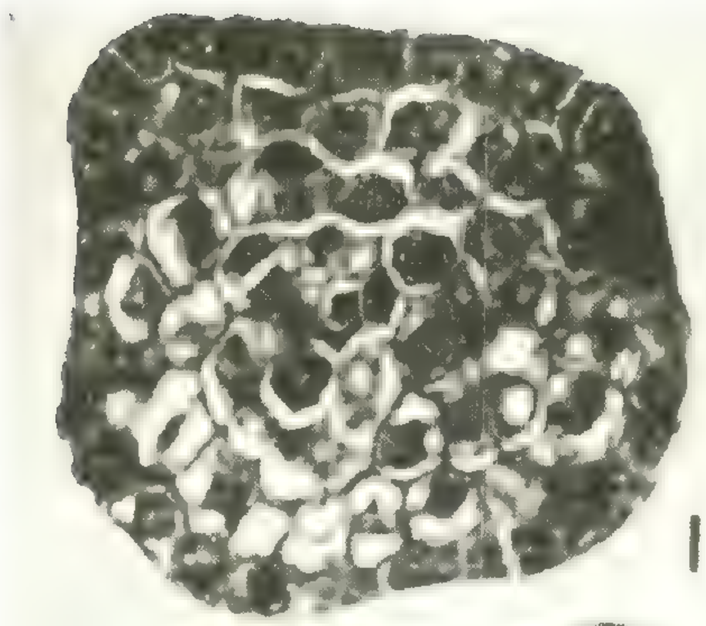
The primodia of the carpels of the annonaceous *Cananga odorata* (Lam.) Hook. f. & Thoms. arise as peg-like projections from the central region of the somewhat flat thalamus. In a transection, each primordium appears as a solid structure. The adaxial part consists of richly cytoplasmic, meristematic cells, but there is a gradually increasing vacuolation in the cells as one proceeds towards the abaxial face (FIG. 1). As development proceeds, the primordium assumes a roughly triangular outline in transection, with a flattened adaxial side and a more or less conical abaxial side. The

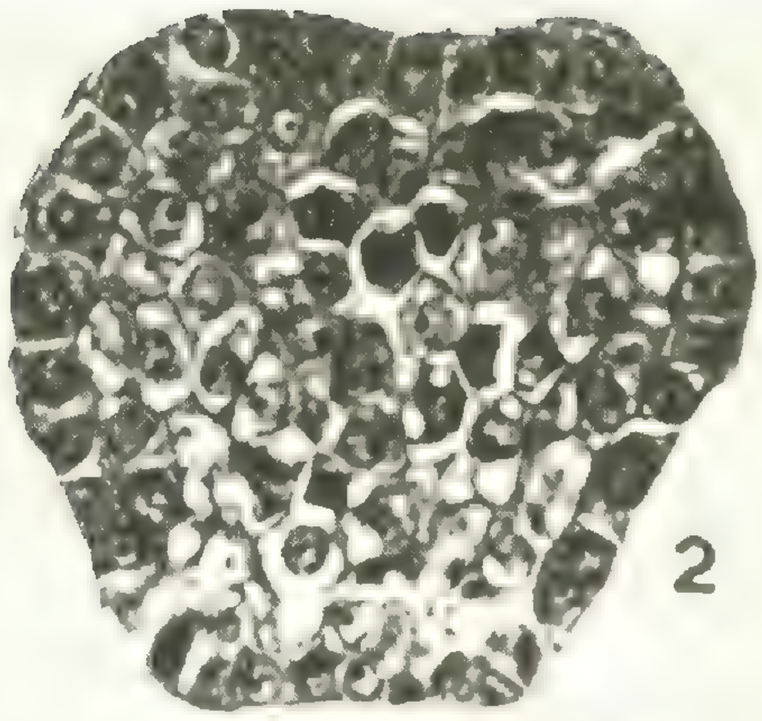
densely protoplasmic meristematic cells become isolated in two masses along the adaxial side. At the same time, a majority of cells in the abaxial part become highly vacuolate and parenchymatous (FIG. 2). During slightly later stages of differentiation, the marked activity of the two masses of marginal meristems (essentially by periclinal divisions) along the adaxial side brings about the formation of a median longitudinal furrow. In a transection, the furrow appears as a notch, and the two free arms consist of active meristematic cells. The procambium of the median vascular strand of the carpel is also noticeable at this time (FIG. 3). The marginal meristems continue their activity for a time, and as a result, the free arms become longer and the furrow deeper (FIG. 4). Soon, however, there is a cessation of the activity of the meristems and this is indicated by the onset of vacuolation in the hypodermal cell layers of the free arms (FIGS. 4, 5).

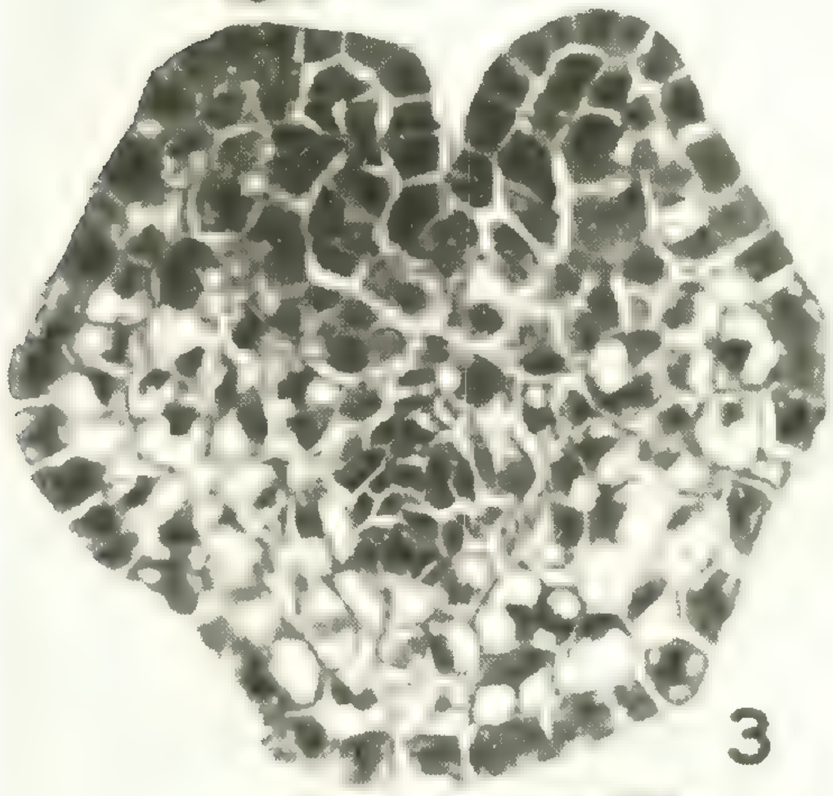
The early ontogenetic stages of the carpel of *Cananga odorata* just described, show striking resemblances to the development of a simple leaf as described by Foster (1936). According to Foster a leaf primordium, soon after its appearance at the growing point, is "pad-like or peg-shaped." Then, "following the early specialisation of the petiolar midrib region in most simple leaves, the lamina begins to differentiate from its upper portion as two thin marginal ridges of meristems." A comparison of FIG. 3 of Foster (1936) with FIG. 3. of our paper makes it evident that the marginal meristems in both structures are not only homologous but also analogous with each other. Continuing, Foster says that, "marginal growth ceases when the main lobes of the lamina have been formed."

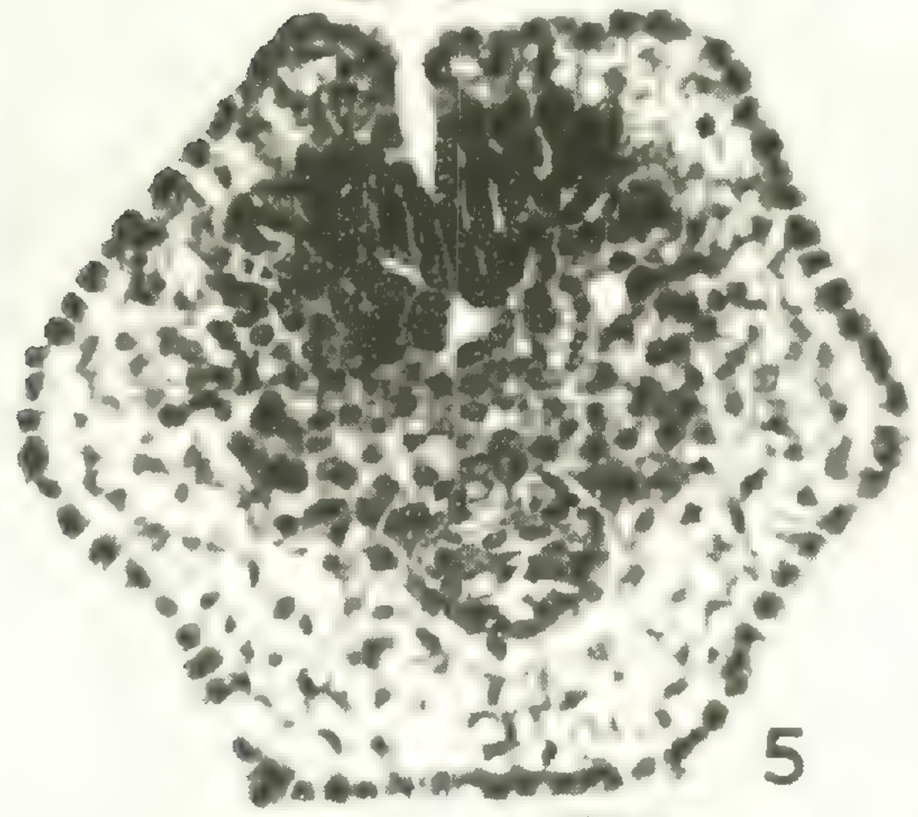
If homology and analogy, which would lead towards a clarification of morphological and phylogenetical ambiguities, may be elucidated from a study of ontogenies, we have here a remarkable exhibition of these principles in the ontogeny of the leaf of angiosperms and that of the carpel of *Cananga odorata*, so that we can clearly comprehend the fundamentally similar nature of the two structures without the interpolation of any speculative hypothesis. The analogy of the early maturation of the marginal meristem shows that in the carpel of *Cananga odorata*, laminal differentiation attains normal completion before the inception of the placental ridges, and at the same time negates the possibility of any assumption of "involute margins." The transection of the carpel of *Cananga odorata* presented in FIG. 4 is a true homologue of a nearly mature, adaxially conduplicate foliar appendage, the entire inner surface of the cleft corresponding to the adaxial surface of the foliar lamina.

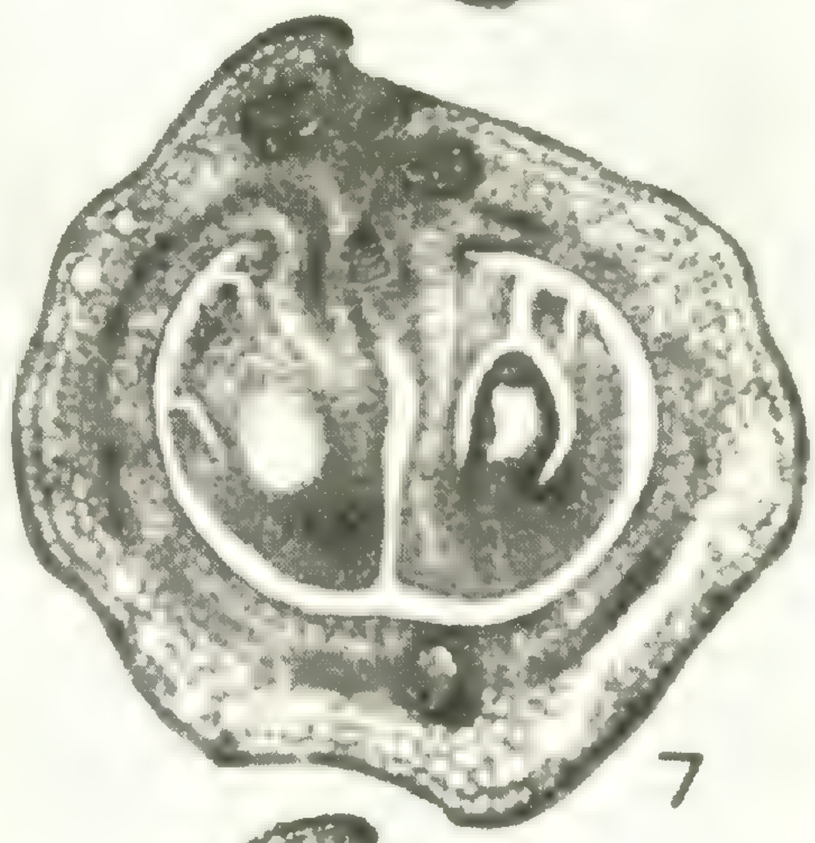
The placental ridges make their appearance soon after or simultaneously with the cessation of the activity of the marginal meristem. The ridges, which develop from the adaxial laminar surface of the carpel by the activity of the two undifferentiated groups of meristematic cells are, in the beginning, situated more towards the centre of each half-lamina and are far removed from the true margins (FIG. 5). This is exactly similar to the condition encountered in *Degeneria* (Swamy 1949), and is probably true of other primitive, unsealed ranalean megasporophylls. Thus, the

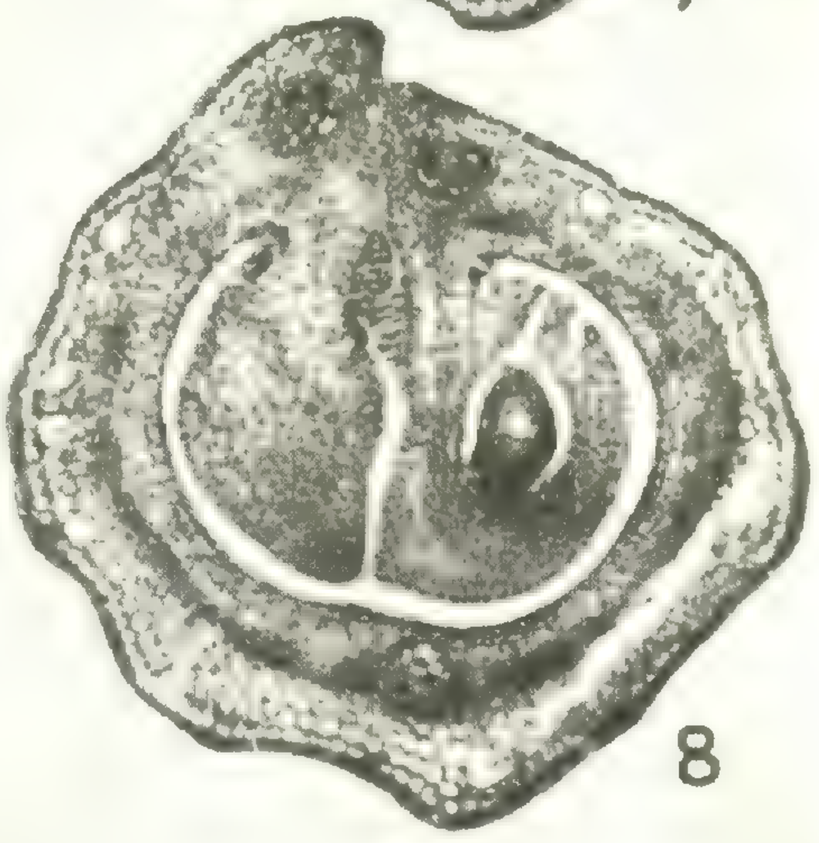












FIGS. 1–6. Transections of the carpel of *Cananga odorata* (Lam.) Hook. f. & Thoms. during successive stages of ontogeny. For explanations see text. 1 × 547; 2 × 540; 3 × 453; 4 × 240; 5 × 270; 6 × 204.

FIGS. 7 & 8. Successive transections of a mature carpel at the time of anthesis, showing the procambial vascular supply to the ovules "given out" from the dorsal trace. × 90.

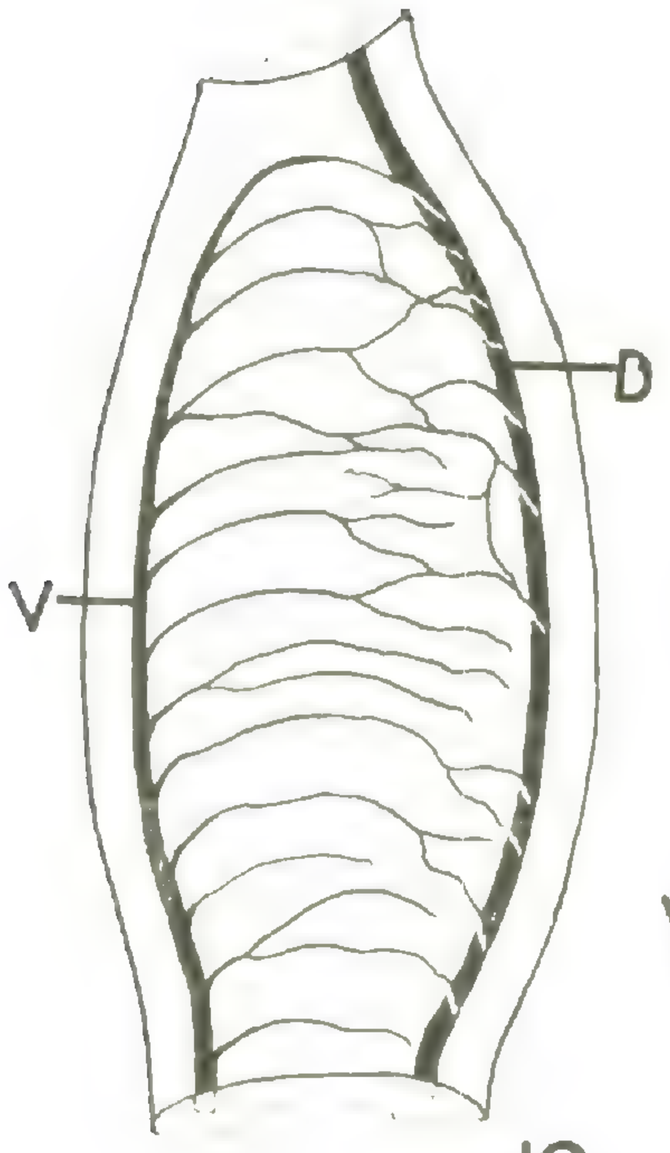
location, as well as the manner of initiation and differentiation of the placental ridges do not suggest a "marginal" placentation, or an "involution" of the true carpellary margins. On the other hand, these ontogenetic successions clearly indicate that the placentation is laminar, and the actual margins are *not* involved in placentation. While in *Degeneria*, *Drimys*, and other relatively primitive carpels the sterile marginal portion of the lamina beyond the place of origin of the placental ridges attains an extensive development in the form of externally flaring stigmatic surfaces, in *Cananga odorata*, there has been a phylogenetic reduction in the activity of the marginal meristem, and consequently of the flaring stigmatic part.

As the placental ridges continue development, the carpel wall undergoes a corresponding abaxial bulging to inclose the cavity of the carpel (FIG. 6). The abaxially directed placental ridges almost fill the cavity of the carpel. The procambium of the ventral vascular strands differentiate within the lamina, at points far removed from the true margins (FIG. 6). As a result of continued abaxial bulging of the carpel wall with a corresponding widening of the cavity of the carpel, the ventral surfaces of the megasporophyll are brought nearer to each other almost to the point of concrescence (FIGS. 6, 7, 9). The ovules differentiate from the rim of the placental ridges.

The developmental changes described above are, however, confined only to the lower, ovule-bearing part of the carpels of *Cananga*. There is very little modification in the upper, stylar and stigmatic regions, where the conduplicate nature remains more or less "set." In these regions, the epidermal cells along the inner surface of the adaxial furrow develop into papillate hairs. A similar differentiation of epidermal hairs takes place also in the ovary cavity around the base of the funicle and in the region of the approximated ventral surfaces of the carpel wall.

It must be emphasized that the ventral surfaces of the carpel do not undergo ontogenetic fusion even during the post-fertilization stages of development. They remain only tightly approximated (FIGS. 7–9). On this account, it is possible to open (at least in the pre- and early post-fertilization stages) the carpel along the ventral suture, thereby exposing the ovules on the corresponding halves. As commented by Bailey and Swamy (1951), the erroneous concept of involute margins and of marginal placentation is obviously the result of taking into consideration only the end products of phylogenetic specialization without a study of the series of successively modified ontogenies.

The remarkable nature of vascularization of the ovules in *Cananga odorata* call for special mention as the situation affords additional evidence in favor of the conduplicate concept. The mature carpel of this plant is supplied with two ventral strands and a single median strand (FIGS. 7–9). Even though the median strand is the first to differentiate in ontogeny, it remains unbranched even in the mature carpel except for strands which vascularize the ovules. The ventral strands, which differentiate comparatively late in ontogeny, are on the other hand, provided (at maturity) with several branches, all of which extend towards the median strand



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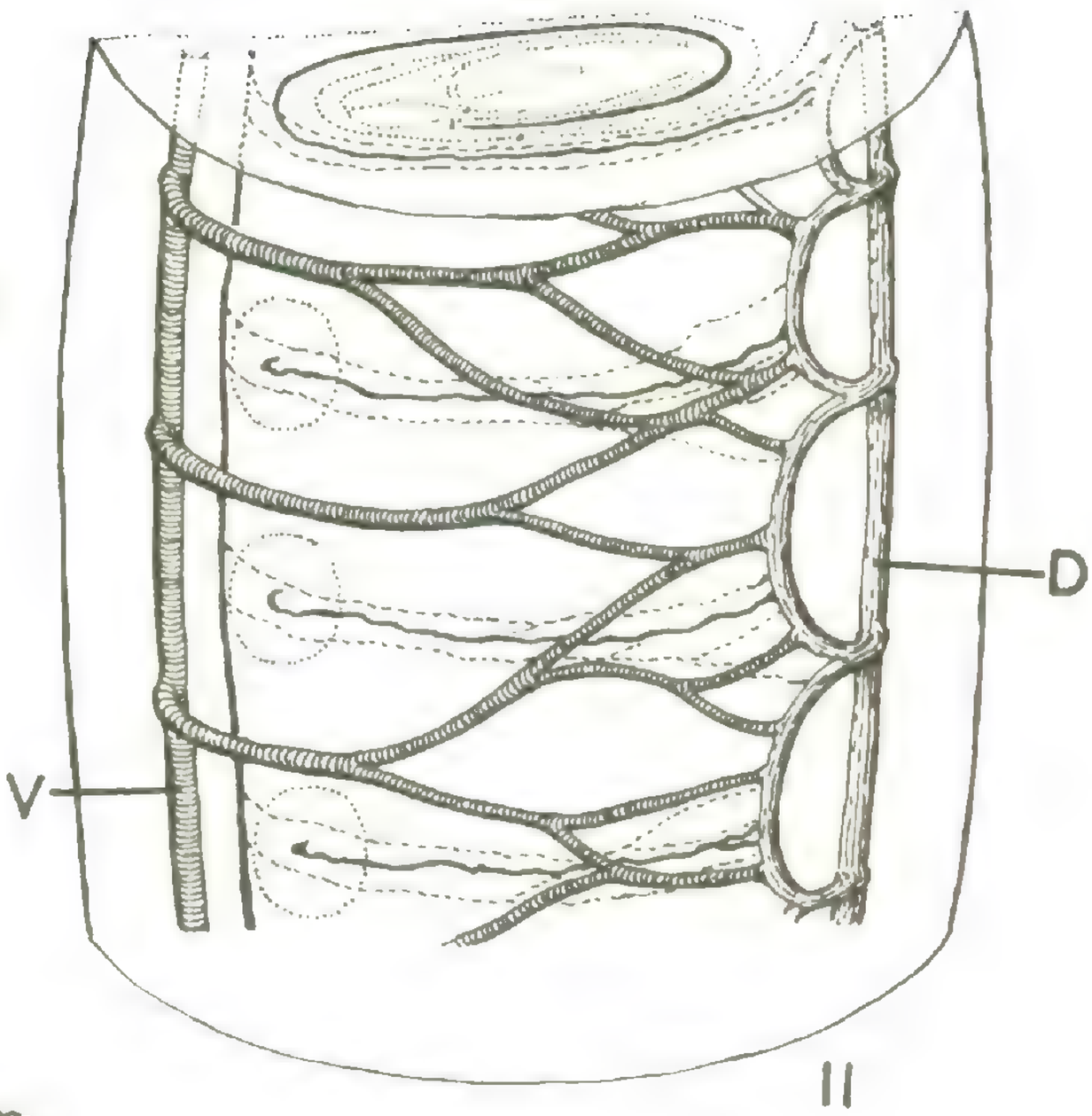

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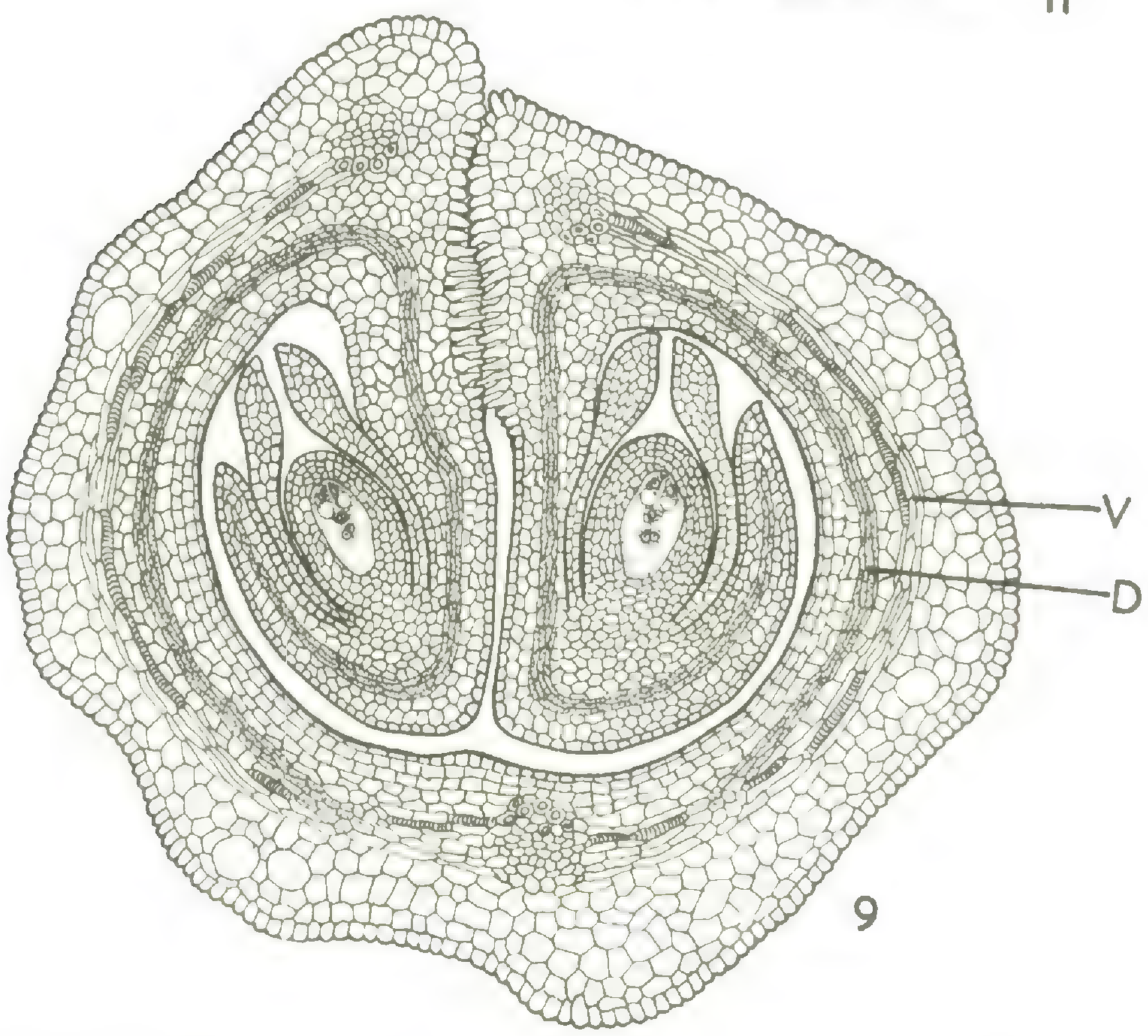

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FIG. 9. Semi-diagramatic representation of the transection of a mature carpel. × 180.

FIG. 10. Vasculature of the mature carpel during anthesis as seen in cleared preparations. Style and stigma removed and only one longitudinal half is shown (Semi-diagrammatic).

FIG. 11. Diagrammatic representation of the vasculature of the carpel during early post-fertilization development as seen in cleared preparations. Only a portion of one longitudinal half is shown. The dotted circles indicate the place of insertion of the funicles. D = Dorsal system of vasculature. V = Ventral system of vasculature.

through the corresponding side of the carpel wall. The branches undergo further proliferation and anastomoses, and some of the ultimate endings establish connections with the median strand (FIG. 10). It must be noted, however, that none of these branches belonging to the ventral system is concerned in the vascularization of the ovules.

The vascular supply to the ovules remains procambial in the mature carpel (at the time of anthesis). It is remarkable that they are supplied from branches arising from the median strand, and *not* from the ventral strands, although the latter are situated nearer to the funicles than is the former (FIGS. 7–9). Thus, as seen in a transection of the mature carpel, the procambial strand, which consists of three to four cell layers in thickness, extends from the funicle directly to the median strand of the carpel through the corresponding side of the wall, and has no connection with the ventral strand of the respective side (FIGS. 7–9). During its course through the carpel wall, the ovular strand lies internal to the ventral system of vasculature (FIG. 9). In the vicinity of the median strand, the ovular trace establishes connection with the anastomoses formed by the short branches of the dorsal system (FIG. 9).

The vascular picture of the mature carpel remains without any profound modifications during early post-fertilization development (FIG. 11). Even after the differentiation of tracheary elements, the ovular strands do not establish connection with those of the ventral system (FIG. 11). Any connection between the two is brought about only very late when the vascular skeleton becomes highly complicated by the development of secondary vasculature in the fruit wall.

The vasculature of the carpel of *Cananga* exhibits an important deviation from other ranalean carpels. In contrast to the condition met with in *Cananga*, it is the dorsal system of vasculature that attains a more extensive development than the ventral system in the mature carpels of *Degeneria*, *Drimys*, and other winteraceous representatives (Bailey and Smith, 1942; Bailey and Nast, 1943; Bailey and Swamy, 1951; Swamy, 1949). The singular nature of vascularization of all the ovules from the dorsal system alone is a unique feature of *Cananga odorata*, and is not known to occur in other ranalean carpels thus far studied. An approach to this condition is, however, seen in *Drimys* and *Degeneria*, where the ovules are vascularized in part by ramifications of the ventral veins, and in part by extensions of the dorsal system of veinlets (Swamy, 1949; Bailey and Swamy, 1951)..

While it is true that vascularization of the ovules by the dorsal system is proof of a laminar placentation, it is interesting that such an anatomical pattern should be retained in the carpels of *Cananga*, which exhibit considerable degree of evolutionary advance in regard to other features. Probably, this situation is yet another remarkable example of the fact that in the *modus operandi* of organic evolution structural changes do not always proceed at a synchronous rate in all the individual features of an organ concerned. Cumulative evidences from comparative morphological studies are becoming increasingly significant and suggest that while an

organ may have undergone structural modifications with regard to certain of the characters, it may remain yet unmodified with regard to other features. In fact, it is the recognition, study and understanding of such "varying segments of salient evolutionary sequences" within the assemblage of extant plants themselves that has recently been of great value in enhancing our knowledge of trends in evolutionary history.

SUMMARY

The early ontogeny of the carpel of *Cananga odorata* is similar to that of a simple angiospermous foliar appendage. A carpel primordium is at first solid and rounded as seen in transections. During development it assumes a roughly triangular outline with a flattened adaxial side. Marginal meristems which function at both corners of the adaxial face bring about the formation of a furrow on the corresponding side, and the two free arms correspond to the lamina of a leaf. The marginal meristem ceases activity at an early stage. Therefore, the laminar margins do not show any evidence of involution. The placental ridges develop from the adaxial surface of the lamina. Just as the ovule-bearing part, the stylar and stigmatic regions of the carpel also exhibit conduplication.

The mature carpel is vascularized by two ventral strands and a median strand. The ventral strands develop a more extensive system of branches than the dorsal. It is remarkable that the ovules are vascularized by branches of the dorsal strand. The ventral strands are not involved in this phenomenon. Such a situation persists even during the early post-fertilization development. The ontogeny of the carpel, the place of origin of the placental ridges, and the unique nature of vasculature of the ovules, are remarkable evidences in favor of the "conduplicate concept" of ranalean carpels. This situation further emphasizes the need for modification of the "Classical View" that looks upon the carpel as possessing involute margins and marginal placentation, and as giving vascular supply to the ovules solely from the marginal (Ventral) vascular strands.

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NEW COMBINATIONS IN HYDRANGEA

ELIZABETH McCLINTOCK

THE FOLLOWING NEW COMBINATIONS, to be used in a monograph of the genus *Hydrangea* (Saxifragaceae), are presented at this time in order to make the names available. Complete synonymy will be included in the forthcoming publication of the monograph.

Hydrangea arborescens L. subsp. **discolor** (Seringe) stat. nov.

Hydrangea arborescens L. var. *discolor* Seringe in DC. Prodr. **4:** 14. 1830.

Hydrangea arborescens L. subsp. **radiata** (Walter) comb. nov.

Hydrangea radiata Walter, Fl. Carol. 251. 1788.

Hydrangea aspera Don subsp. **strigosa** (Rehder) comb. nov.

Hydrangea strigosa Rehder in Sargent, Pl. Wilson. **1:** 31. 1911.

Hydrangea aspera Don subsp. **robusta** (Hooker f. & Thomson) comb. nov.

Hydrangea robusta Hooker f. & Thomson, Jour. Linn. Soc. Lond. Bot. **2:** 76. 1858.

Hydrangea aspera Don subsp. **sargentiana** (Rehder) comb. nov.

Hydrangea sargentiana Rehder in Sargent, Pl. Wilson. **1:** 29. 1911.

Hydrangea anomala Don subsp. **petiolaris** (Siebold & Zuccarini) comb. nov.

Hydrangea petiolaris Siebold & Zuccarini, Fl. Jap. **1:** 108, *t. 54.* 1840.

Hydrangea scandens (L. f.) Seringe subsp. **liukiuensis** (Nakai) comb. nov.

Hydrangea liukiuensis Nakai, Bot. Mag. Tokyo **25:** 63. 1911.

Hydrangea scandens (L. f.) Seringe subsp. **chinensis** (Maximowicz) comb. nov.

Hydrangea chinensis Maximowicz, Mem. Acad. St. Petersb., ser. 7, **10**(16): 7 (Rev. Hydrang. As. Or.). 1867.

Hydrangea scandens (L. f.) Seringe subsp. **kwangtungensis** (Merrill) comb. nov.

Hydrangea kwangtungensis Merrill, Jour. Arnold Arb. **8:** 7. 1927.

Hydrangea macrophylla (Thunberg) Seringe subsp. **stylosa** (Hooker f. & Thomson) comb. nov.

Hydrangea stylosa Hooker f. & Thomson, Jour. Linn. Soc. Lond. Bot. **2:** 75. 1857.

Hydrangea macrophylla (Thunberg) Seringe subsp. **chungii** (Rehder) comb. nov.

Hydrangea chungii Rehder, Jour. Arnold Arb. **12**: 69. 1931.

Hydrangea section **Euhydrangea** subsection **Macrophyllae** subsect. nov.

Flores albi, caerulei, vel carnei; ovarium inferius ad anthesin, ½ superius in fructu, capsula apice conica; stylis connatis usque ad medium vel minus profunde partitis.

TYPE SPECIES: *Hydrangea macrophylla* (Thunberg) Seringe.

THE DIRECTOR'S REPORT

The Arnold Arboretum during the Fiscal Year ended June 30, 1956

By tradition the report of the Director of the Arnold Arboretum is published in the October issue of the Journal of the Arnold Arboretum and of late years has been distributed as well to the Friends of the Arnold Arboretum. The report, therefore, is written at the beginning of the summer, usually after the rush of activities of a busy spring. It is natural that the beauty of the Arboretum grounds during the past few months is foremost in the director's mind as one of the outstanding events of the past year. Spring was late in its arrival at the Arboretum in 1956 and the flowering season was characterized by one of the most unusual mixtures of flowering periods on record for Jamaica Plain. With forsythia and lilacs in nearly full bloom at the same time and with the lingering flowering of magnolias and normal flowering of various species of azalea there were many combinations of color and beauty never before recorded on our grounds. The grounds staff was able during the fall and winter to complete a backlog of pruning made necessary by the hurricanes of recent years, thus bringing the grounds to top condition. With the cooperation of the Boston Park Department in improving the appearance of the walks and roadways, one often heard the public comment, "The Arboretum has never looked as attractive as it does now."

The Staff:

The staff was saddened during the past year by the death of its Director *Emeritus*, Elmer Drew Merrill, on FEBRUARY 25, 1956. Dr. Merrill's long and active career in contribution to the knowledge of the Pacific area vegetation was reviewed in the July issue of the Journal of the Arnold Arboretum. His service to the Arboretum and to botany at Harvard was significant. With his appointment in 1936, he undertook to coordinate or combine, for greater efficiency and economy, the activities of nine separately endowed botanical organizations at Harvard. He was appointed the first "Administrator of Botanical Collections" and was supervisor of the Arnold Arboretum. Under his direction the Arboretum expanded its program of study in Asiatic vegetation and increased both its library and herbarium resources of this area. His own research interests in the Orient allowed him to guide with personal attention the exploration and collections of many young botanists. The outbreak of the second World War prevented the implementation of the plans Merrill had prepared for the union of botanical resources at Harvard and it was only after his retirement that his administrative ideas were carried out. The war effort, however, again demonstrated the practical value of the botanical information inherent in the herbarium collections and library necessary for the study of plants and

Merrill's several books on emergency food plants and the educational and recreational guides to the biology of the Pacific area drew just praise. Dr. Merrill retired as Director of the Arnold Arboretum in 1946 and as Arnold Professor of Botany in 1948, at the age of seventy-two. It was then that he received his first Guggenheim Fellowship, an award usually reserved for younger men, to make possible several trips to European herbaria and a continuation of his studies. Unfortunately, a series of heart attacks limited his activities and led ultimately to his death. Tributes and honors to Elmer Drew Merrill have been received at the Arnold Arboretum from many of the societies and fellowships to which he belonged. He was known around the world, as recent tributes from institutions as far separated as the Academy of Sciences of the Philippines from the Académie des Sciences in Paris will testify.

It is also with regret, but with appreciation for their services, that I announce the retirement and resignation during the fiscal year of Miss Hariklia Yeranian in July of 1955 and Mrs. Beatrix Farrand during the winter months. Miss Yeranian, a mounter of specimens at the Arnold Arboretum for thirty-two years, saw the development of the herbarium to its stature of today. Beatrix Farrand, noted horticulturist and long a friend of the Arnold Arboretum, was appointed consulting landscape architect in 1945 and contributed valuable services in the necessary revamping of the grounds following the unavoidable neglect of the war years. Through her vision the Arboretum has vistas, groupings and patterns of color for all to enjoy on the grounds.

Two botanists were added to the staff of the Arboretum during the past fiscal year to work on special projects supported wholly or in part by special grants. Dr. Robert Bennie Channell, who received his Doctor of Philosophy degree from Duke, joined the staff to work with Dr. Carroll Wood on the vegetation of the southeastern states. This work is supported in part by grants from the National Science Foundation and by the George R. Cooley Fund for work in taxonomy of flowering plants.

Dr. Ding Hou received his doctorate from Washington University in St. Louis, where he worked under Dr. Robert Woodson in preparing a revision of the genus *Celastrus*. Dr. Hou accepted a one-year appointment at the Arboretum to assist on the Flora of China project which has been supported by grants from the China International Foundation.

Honors came to several staff members during the year. Professor I. W. Bailey was elected a foreign member of the Linnaean Society of London and an honorary member of the Indian Botanical Society. Dr. Donald Wyman continued his services as a Trustee of the Massachusetts Horticultural Society and was elected secretary of the American Horticultural Council, succeeding in that office Dr. George Lawrence of the Bailey Hortorium. Dr. Howard was elected to serve a one-year term as one of the Directors of the American Association of Botanical Gardens and Arboretums. Dr. Kobuski was re-elected Assistant Curator of the herbarium of the New England Botanical Club and continued to serve on the council of that organization. Dr. Wood accepted the secretaryship of the Syste-

matic Section, Botanical Society of America in preparation for the meeting of the American Institute of Biological Sciences to be held in Storrs, Connecticut, in 1956.

Members of the staff, both officially and informally, represented the Arboretum at horticultural and botanical functions on both sides of the Atlantic during the past year. Dr. Howard attended the Fourteenth International Horticultural Congress held in the Netherlands. His visit to European gardens will be described later in this report. Dr. Sax and Dr. Wood attended annual meetings of the American Institute of Biological Sciences in East Lansing, Michigan, in September. Dr. Donald Wyman represented the Arboretum at meetings of the American Horticultural Council and the American Association of Botanical Gardens and Arboretums held jointly in Philadelphia. Mr. Coggeshall attended the meeting of the Plant Propagator's Society in Cleveland, where he presented a feature paper on the propagation of Asiatic maples. Dr. Karl Sax was chairman of the opening session of the Brookhaven National Laboratory Genetics Symposium and attended the American Society of Horticultural Sciences Conference on root-stocks held at Monmouth, Maine. He also presented papers at the Northeast Regional Meeting of the American Society of Horticultural Sciences held at the Biological Laboratories in Cambridge during the winter.

The requests for staff members of the Arboretum to speak for meetings of garden clubs and groups interested in the work and resources of the Arboretum and its staff continued to exceed our ability to fulfill. Such extension services must, of necessity, remain an extracurricular activity of the Arboretum staff members. Even so, staff members travelled widely and spoke to many groups on a wide variety of topics. Dr. Howard presented one of the Science Lectures in the winter lecture series at the Fairchild Tropical Garden in Miami, Florida, while en route to Jamaica for field work. On the same trip he spoke to garden clubs in Daytona Beach, Hobe Sound and West Palm Beach and to Harvard Clubs in Jacksonville, Winter Park, Miami and St. Petersburg in Florida and in Birmingham, Alabama. In addition to this schedule, he lectured to other groups in several of the New England States. Dr. Sax and Mr. Coggeshall each took part in the lecture series of the Massachusetts Horticultural Society in Boston. Mr. Coggeshall spoke for the Massachusetts Nurserymen's Short Course, for the Gardeners and Florists Club of Boston and also to the Rhode Island Nurserymen's Association. Dr. Wood described the activities of the Arboretum to Harvard Clubs in Massachusetts and in North Carolina and Dr. Wyman and Mr. Williams lectured on subjects of their specialty to garden clubs in several New England States. The Arboretum is fortunate in being so well represented by capable speakers.

Horticulture:

Again this past year the weather of New England has varied from that expected and so has been an important factor in the growth and maintenance of the plants at the Arboretum. During the summer sustained rainy

FIG. 1. Flooding in the Arnold Arboretum during the heavy summer rains, 1955. Both pictures taken on August 19th.

TOP: Bussey Brook looking towards Walter Street Gate with the water reaching the road.

BOTTOM: Flood waters in the Linden collection near the *Cercidiphyllum* across from the Meadow Road.

periods, especially those associated with hurricane "Diane," produced flooding in many parts of the grounds and caused the Bussey Brook to run high and wash out its retaining walls in several places. The floods themselves did not do serious damage but the saturation of the ground, with accompanying gusty winds, even though low in velocity, caused the loss of several trees which had been weakened in previous seasons by hurricanes. We notice especially the loss of a specimen white oak across from the collection of mountain laurels which leaned for many years towards Bussey Brook. It was under this tree that a memorial service for Charles Sargent was held in 1927. This magnificent oak, which withstood the severe hurricanes of 1938, 1953 and 1954, fell during an eleven-inch rainfall in the summer of 1955 and of course could not be re-established.

The high water table lasted into the fall and winter and the freezing and thawing of the early months of 1956 produced further standing water in parts of the Arboretum. The linden collection, located in a natural low spot along the Meadow Road, appears to have been affected by this standing water and several of the larger trees show signs of considerable damage. In addition, mould became prevalent in the turf of that area and required special treatment.

One of the latest freezes on record occurred on May 25th in Jamaica Plain and was also felt at Weston. This late freeze caused minor damage to the leaves and flowers normally open at that time, but, insofar as is known to the present, will have no lasting effects on the ornamental plantings in Jamaica Plain. The apple crop at Weston, however, is a total loss this year because of the freeze.

The destructive effects of the torrents of water which poured down Bussey Brook, crossing above the road at the rhododendron collections and washing out the retaining walls, have required special consideration. Several of the plantings in the rhododendron collection lost soil from around the roots. Erosion is also evident at the golden larch plantings. As the maintenance of such storm sewers is the responsibility of the Boston Park Department, this condition has been called to their attention and some work was started on replacing the retaining wall during June.

The appearance of the grounds, particularly near the lilac collection, was greatly enhanced this year when the Park Department found it possible to clean out the grass and soil from a portion of the cobblestone gutters which line the roads. This task has been neglected since before the War. The accumulation of silt and the encroachment of grass and weeds made maintenance of the collections difficult, thus detracting from the appearance of the grounds. The workers of the Park Department started at the collection of viburnums and cleared down to the forsythias. The Arboretum crew continued the work to the Forest Hills Gate and also edged all the sidewalks from the Forest Hills Gate to above the lilacs. The Park Department also repaired the macadam sidewalks, improving the appearance and increasing the safety of these paths. Again, neglect and lack of care in recent years had created unsightliness and hazard in the tussock growth of grass in the sidewalk areas.

FIG. 2. The Sargent cherry near the pond at the Forest Hills Gate was badly broken during the hurricanes of 1954 and had to be removed. A large specimen was moved by the Arboretum staff to a more favorable spot on the edge of the same pond.

Special attention has been given to the plantings at the summit of Bussey Hill. Many of these shrub plantings had become overgrown and filled with weed trees. The valueless plants were weeded out of these areas and many of the approaches to the turn-around area were planted in ground covers which will improve the appearance of the area and at the same time demonstrate many of the better ground covers in natural settings, to contrast with the comparative row plantings of Weston.

The collection of rhododendrons has responded so well to the applications of fertilizer and, in particular, to castor pumice applied in the past two years, that additional supplies of this fertilizer were added to the mountain laurel collection and to various plantings of azaleas. The collection of *Rhododendron calendulaceum* bloomed especially well this year, indicating that the treatments given have been correct. The overgrown collection of Ghent hybrid azaleas also received special attention during the fall. The resulting bloom in the spring was spectacular. Both of these collections were outstanding in their excellent natural setting among the oaks.

During the last year the Arboretum was troubled with a severe infestation of rhododendron scale which resisted control with the usual sprays and methods of application. This scale was tentatively identified as one of the Kermes scales which invades the crevices of the bark. The mature scales are extremely difficult to kill. It was recognized that an attack on the hatching scales would be the only satisfactory method of control. Applications of two pounds of 50% wettable DDT and two pounds of 25% malathion wettable powder in 100 gallons of water were made with a power sprayer to allow the spray to run down all the branches and twigs. Applications made on June 20, July 8 and August 1 seemed to give almost complete control of this pernicious pest. The only other disease of consequence in the Arboretum has been the outbreak of fire blight on crab apples and other members of the Rosaceae, but control by the new antibiotics appears to be effective, although expensive at the present time. During the year applications of milky spore disease, under the trade name of "Doom" were made to the lawns and grassy areas within the Arboretum. It is hoped that this attack on the Japanese beetles will reduce their numbers within a few years. In the meantime, spraying with insecticide was continued to counter the ravages of these insects, primarily on members of the Rosaceae.

Among the items of equipment purchased in the fiscal year were a mechanized rotary soil screen to make possible the use of street sweepings and leaves deposited in our dump by the Street Department of the City of Boston. A double disc was purchased to facilitate cultivation in the shrub collection. A new two-ton Chevrolet truck with a dump body and a winch was a needed item to replace an old Army truck purchased in 1948 from Army surplus. A new type of lawn mower with a rotary blade called a "Snappin' Turtle" was obtained to replace the reel-type mower used along the walks and in the shrub and lilac collections. The new machine not only has a reverse drive, making it easier to handle, but will cut taller grass than our older machine.

Two hundred and twenty species and varieties were added to the collec-

tions in a fall and spring planting program. Of these, seventeen appear to be completely new to American gardens and forty-nine additional ones have never been tried at the Arnold Arboretum. The remainder, in some cases, duplicate plants already in our collections, but represent additional clones for trial, while others represent taxa which have been grown at the Arboretum in the past but have died out or have been lost.

Dr. Wyman continued to act as coordinator for a group of American arboreta and botanic gardens by working in conjunction with the Horticultural Crops Research Branch of the U.S. Department of Agriculture in bringing into the United States for trial plants now on the "prohibited list." One hundred and forty-five plants have been introduced and grown for two years at Glen Dale, Maryland, to satisfy the Bureau of Plant Quarantine Regulations. They have now been released to interested arboreta for propagation and distribution. Fifteen taxa were released for the first time this year.

Four plants were propagated and offered for distribution to nurserymen in continuation of the Arboretum's program of making the best ornamental plants available for commercial distribution. Thirty-six nurserymen in the United States, Canada, England and the Netherlands accepted plants under the terms of agreement to propagate from the plants supplied. The origins of the four plants, *Magnolia loebneri* cv. "Merrill," *Crataegus monogyna* var. *inermis*, *Pyracantha coccinea* cv. "Kazan" and *Cornus alba* var. *sibirica*, are of interest. *Magnolia loebneri* is a hybrid species known in Europe since its first production around 1885. The best features of the two parents, *Magnolia stellata* and *M. kobus*, appeared in the hybrid. Unfortunately, the hybrids introduced into the United States did not prove desirable or hardy in the Boston area. The same parents were crossed by Dr. Sax at the Arboretum in 1935 and the most desirable selection from this cross was given the cultivar name honoring Dr. Elmer Merrill. *Magnolia loebneri* cv. "Merrill," therefore, is a new selection of a cross which has long been known. Of a different origin is *Crataegus monogyna* var. *inermis*, an excellent but little known thorn-apple which has been under cultivation at the Arboretum since 1914. The staff felt that this plant should be better known; hence its selection for distribution to cooperating nurserymen. The remaining two plants offered, *Pyracantha coccinea* cv. "Kazan" and *Cornus alba* var. *sibirica* are recent introductions of the Arnold Arboretum from Europe. It is felt that the former, although still under trial, will prove to be more hardy than any other fire thorn. The latter was selected as true to type, for many inferior plants, incorrectly named, are being grown under this name throughout the country. This stock distributed by the Arboretum will assure nurserymen of a re-established standard plant, accurately determined.

In addition to plants which were sent to cooperating nurserymen, the Arboretum has filled many requests for plant materials and plant parts from literally all sections of the world. Requests for materials from the living collections varied from pollen for identification and breeding programs to seeds and propagating material to herbarium specimens and pre-

served or fresh material for scientific study. These requests are filled as time and personnel permit. During the past fiscal year the propagator distributed on request ninety-four shipments of seeds representing three hundred and twenty-two species and varieties. These were sent to eleven countries besides the United States and Canada. In addition, one hundred and fifty-one shipments of four hundred fifty-six species and varieties of whole plants or cuttings and similar parts for propagation were sent to four different countries outside of the United States. Such shipments involve time and often considerable routine labor for preparation and may also be expensive when shipments must be sent by air to insure the materials of safe arrival in living condition. Many of the shipments are offered in exchange and many other gardens and arboreta ship, with or without warning, plants or seeds for trial plantings. Thus, during the past year the Arboretum received both by request and without requests one hundred forty shipments of plant parts, representing five hundred sixteen species and varieties.

During the past year it has been possible to establish a working procedure with several gardens and arboreta in the Southeastern United States and in the Caribbean. Now, when seed shipments are received, sizeable quantities are divided and portions of the seed-lot are shipped to more southern institutions for trial. If seed-lots are small, the plants are started in our greenhouses and the quantity of young plants are divided, a portion to be tried for hardiness in our own area and others to be sent for trial further south. We hope by this method to carry through to maturity many of the species and varieties sent to us for trial which in the past have been frequently lost when the young plants were killed by severe winters. At the same time the chance of a hardy strain surviving the New England climate has not been eliminated.

For our own collections, for distribution and for experimental purposes, the propagator increased by cuttings, grafts and budding 15,516 individual plants, representing four hundred seventy-five species and varieties. As the plants propagated were often in excess of our own needs, many were distributed informally for testing purposes through the educational program. In addition, when circumstances permit, the Arboretum will cooperate with outside organizations for worthwhile purposes. Specimen trees were made available for public plantings at several New England libraries during the past year and in response to a special request the Arboretum was pleased to cooperate with the Boston Art Festival Committee. This Committee wished to make a gift of a tree to the City of Boston for the Boston Public Garden. The director felt that the Public Garden should have the most recent "living fossil," *Metasequoia glyptostroboides*, a plant introduced by the Arnold Arboretum, to complement and accompany the older "living fossils," *Ginkgo biloba*, which are present in the Garden. A large tree of the original introduction fortunately was still available in a nursery plot at Weston. The tree was fourteen feet tall, too large for the Arboretum staff to handle; hence it was moved by a professional arborist at his own expense, during the festival. In spite of the

dry weather and the out-of-season transplanting, our latest observation indicates the operation to be a complete success and the tree is growing well in its new location.

Many of the surplus plants grown at the Arboretum find a place on the grounds around the Harvard University Buildings in Cambridge. Surplus shrubs ranging from three to eight feet high and trees six to ten feet high were selected by the Department of Buildings and Grounds from a list of ninety-two species which we felt were desirable for campus plantings. This distribution of surplus plants was mentioned in the original indenture establishing the Arnold Arboretum. Such plantings not only beautify the Harvard campus, but increase the student interest in horticulture and the proper selection of plant materials for landscape and garden design.

We continued a program of renovation of buildings belonging to the Arboretum in Jamaica Plain and Weston. During the year the Administration Building required repairs to the heating system and received new downspouts of heavy copper, as well as a complete outside painting of all exposed wood surfaces. The new rainspouts were badly needed.

The regular work of labelling and mapping the grounds and the checking of records continued throughout the year. Special characteristics of the plants or unusual responses are noted on the records in the master file. Additional photographs were taken of the grounds, the operations and the plants. These consisted of negatives and prints in monochrome and transparencies in thirty-five millimeter kodachrome and larger ektachrome. Photographs and prints are made available on request and are used in publications by the staff, as in Dr. Wyman's recent book on ground covers. The color transparencies have been reproduced in several national horticultural magazines and several were the bases for the drawings of ornamental shrubs and trees which appeared in Life magazine during the past year. The large sign sponsored by the Boston Envelope Company honoring the Arboretum was based on kodachrome slides in our files.

During the year Dr. Wyman was elected secretary of the American Horticultural Council and as a result the Arnold Arboretum has become the official headquarters and letterhead address for this organization. Dr. Wyman was able to complete and ready for publication his book, Ground Cover Plants.

The Fourteenth International Horticultural Congress was held in Scheveningen, the Netherlands, during August of 1956. Dr. Howard, who attended as representative of the Arnold Arboretum, was also able to visit many other botanical gardens and arboreta in Europe. His trip included visits to the Botanic Garden of the Riksmuseum in Stockholm and the old gardens at Charlottenlund in Sweden. In Denmark he visited the herbarium and the botanic garden, as well as the University gardens in Copenhagen, and made a special trip to northern Denmark to see the private botanic garden of the late Dr. Borgesen and to study some of the government forests in the area. Travelling by airliner made it possible for Dr. Howard to make short visits to the botanic gardens in Hamburg, Berlin, Hanover, Göttingen and Munich in Germany. After arriving in Zürich and visiting the

botanic garden of the University, Dr. Howard was invited to accompany Dr. Däniker, the director of the garden, on a trip across the Alps to Lake Maggiore and the newly-established botanic garden on the island of Brissago. This island garden, a short boat ride from Lucarno, features tropical and subtropical vegetation within sight of snow-capped mountains and glacial streams. His trip continued across northern Italy and across the Alps, this time by train, down the Rhone valley to Lucerne and Geneva, where he visited the botanic gardens in order to study the formal plantings so well done by the Department of Parks in the city of Geneva.

FIG. 3. The first general assembly of the Fourteenth International Horticultural Congress held at Scheveningen, the Netherlands, August 1955. Dr. Howard represented the Arboretum at these meetings.

The Horticultural Congress was held at the sea-side village of Scheveningen, just outside the Hague, which serves as headquarters for many international congresses. Excursions and visits were arranged before and during the Congress for the many visitors from abroad. Delegates and members attending the Congress far exceeded expectations and taxed the limited housing facilities to the utmost. However, the hosts met the situation and conducted an enjoyable and extremely well-executed Congress. Dr. Howard attended the pre-congress sessions of the Committee on Horticultural Nomenclature and Registration and, along with Dr. George Lawrence of the Bailey Hortorium, shared the distinction of being the only American horticulturists in these important sessions. The Committee

was unable to complete its discussions before the Congress convened and therefore held evening meetings during the scheduled program. Dr. Howard served on the subcommittee appointed by the chairman to draw up the resolutions for the Congress as a whole and he also agreed to serve on behalf of the Arnold Arboretum in an effort to compile a directory of privately maintained systematic listings of cultivar names and to report on such a list at the next Congress.

Excursions during the Congress took members to various parts of the Netherlands. Visits to the old arboretum at Boskoop, to Belmonte, the new arboretum, and to the commercial nurseries in the area proved most interesting. Comparisons in size of the collections at the new arboretum made by its director with the collections of the Arnold Arboretum proved embarrassing, as well as amusing. The removal of Dr. Sargent's collection of *Crataegus* from the slopes of Peter's Hill in Jamaica Plain was not known to the director of the Dutch Arboretum. It was a surprise to him to learn that his little Arboretum now contains more species and varieties of both *Crataegus* and *Sorbus* than does the Arnold Arboretum. Exchange of plant materials between gardens and nurseries in the Netherlands and the Arnold Arboretum have been many and frequent in the past and, with an appreciation of the resources of each area, will continue so in the future.

A high point of the Congress came near the close when the entire membership was taken to Amsterdam to attend the Alsmeer flower parade held in the Olympic stadium. This show, based on a theme of sound and color, with floral floats interpreting classic works of music, lasted three hours and was followed by a boat ride through the canals of Amsterdam.

The Congress offered the director an opportunity of meeting many horticulturists from remote sections of the world for the first time and of renewing acquaintances with others. After the close of these meetings Dr. Howard visited London, spending some time at Wisley and Kew and then travelled to Edinburgh to take part in the meeting of the Systematics Society of Scotland held at the Edinburgh Botanic Garden.

The trip was pleasant and profitable. It was obvious that American gardens such as the Arnold Arboretum can never compete in appearance with European gardens where meticulous hand labor is more available and more reasonably priced. The schools for gardening apprentices and students which supply much reasonable labor would not be feasible at the Arboretum. Also obvious was the difference in the consideration of the general public for the plants and plantings generally seen in Europe in contrast to our own experience in New England. Nevertheless, the Arnold Arboretum can be proud of the scope of its collections, the quality of the plants and especially the standards of labelling and accuracy of names in the living collections. In these characteristics, few European gardens even approach the Arnold Arboretum and none equals it.

The experimental work of the Arboretum staff dealing with ornamental plants on the grounds and in the greenhouses continued. Experimental and comparative methods of weed and brush control are always possible and, in fact, necessary to maintain the plantings. Special attention was again given

to control methods for *Cynanchum nigrum* and species of *Convolvulus*. Dr. Wood has under observation selected clones of *Robinia*, the rose acacia, both for basic information of the species relationships of the clones and for their possible ornamental value as individuals and as breeding stock. In the greenhouses Mr. Coggeshall continued his experiments on control of germination of seeds, propagation by cuttings, comparability of stock and scion and evaluation of propagation techniques. The intermittent mist propagation system given to the Arboretum for experimental purposes last year has been established and used for comparative propagation experiments with the plastic "tent" technique and other selected methods. Seeds of *Cotoneaster*, *Viburnum*, *Chionanthus* and *Hamamelis* have been subjected to tests designed to overcome double dormancy through the use of concentrated sulfuric acid. Seeds of *Laburnum* and *Albizzia* have received treatment with hot water and concentrated sulfuric acid to determine comparative effects of these treatments in germination. A number of *Rhododendron fortunei* hybrids of known rooting capability have been used to test the effects of types of media and wounding practices on the rooting of cuttings. An evaluation has been attempted of a new method of propagation using sphagnum moss and plastic by comparison experiments. Experiments of the compatibility of understocks and the treatments necessary in making successful grafts have been conducted with *Pinus* and *Picea* species. After one run was completed a letter was received from Australia asking for exactly the information which that experiment was designed to test. Thus by coincidence the Arboretum was able to supply new experimental data. A number of experiments are in progress to determine the effects which different temperatures, maintained for differing lengths of time, have upon the germination of such tree seeds as *Acer*, *Carpinus*, *Quercus*, *Magnolia*, *Cornus* and *Pseudolarix*. Many of the experiments mentioned are designed to provide the answer to problems long facing the Arboretum and the commercial nurserymen. Other experiments are designed to supply more scientific answers as to why plant materials must be handled as they are to respond as desired.

Finally, mention should be made of a development which will affect both the appearance and the problems of maintenance of the Arnold Arboretum in the future. During the year the City of Boston sold the land known as Joyce Kilmer Park, which is at the junction of Walter and Center Streets. This was deeded directly to the City of Boston and has never been a part of the Arboretum. This piece of wooded land is across from the conifer collection on Walter Street and adjoins the Weld-Walter Street tract of the Arboretum. The Park was sold to the trustees of the Dorchester Home for the Aged and, although the sale was protested by residents of the area, the sale was approved by the Supreme Judicial Court of Massachusetts. The trustees plan to erect on this site a large building tentatively known as the Hebrew Home for the Aged in West Roxbury. The large building will occupy most of the space available in the plot. As construction proceeds in the next year the traffic problem will be accentuated and when completed the service traffic and visitors to the Home will present additional

problems to be faced by the Arboretum staff. It is hoped that this building and its surrounding area can be landscaped so that it does not clash with the natural beauty of the adjacent Arboretum property. The Director of the Arboretum plans to remain in touch with the contractors and the trustees to work out mutual problems which will arise due to this significant change along Centre Street.

The Case Estates:

The horticultural work of the Case Estates in Weston continued without interruption during the year. Damage from floods, windstorms and frost was minor, excepting only the loss of the experimental apple crop due to a late May frost during the flowering period. Several of the buildings on the grounds were given additional attention during the year and one large house and adjacent land, left for the use of Mrs. Theodore Chandler by the will of Miss Marion Roby Case, reverted to the Arboretum when vacated by Mrs. Chandler in February of 1956. With the approval of the Corporation, this house is currently being renovated and will be occupied by the Director of the Arboretum in the fall.

The spring season was very slow in developing at Weston and the open house scheduled on the grounds for May 5th did not show the plants and plantings to the same advantage as did the comparable date of the year before. However, with excellent publicity, including location maps and directions published in the Sunday papers, the attendance was high despite inclement weather. Special attention was called by the newspapers and by an issue of Arnoldia to the collection of street trees and other small ornamental trees which have been established now for five years. This collection is located to the rear of the ground cover plots along the road to the town swimming pool and draws nearly as many visitors annually as does the better known ground cover display plot.

Some display planting of crab apples was done in the open field across from the Weston High School and one new area near the barn was developed for the collection of *Robinia* clones under study by Dr. Wood.

Education Program:

The informal education program of classes for adults held at the Arboretum was continued in two semester sessions during the past year. The interest in these courses remained high and the classes probably have the highest perfect attendance ratio of any education program in Boston.

During the fall the following classes were offered by Arboretum staff members: Basic Botany for the Home Gardener, Dr. Wood; Fall Field Class, Dr. Wyman; Plant Propagation I, Mr. Coggeshall; and Principles and Practice of Plant Identification, Dr. Howard. Mr. Coggeshall's classes in plant propagation proved so popular that three sessions were offered again. The subject matter was divided between fall and spring so that topics for practice and immediate use could be taught at the appropriate time. Dr. Howard's class was new to the program and was designed to familiarize students with the use of keys, manuals and descriptions of

cultivated plants and to recognize the larger groups of cultivated plants by the morphological characters that define and distinguish them.

Two new classes were added to the spring program of education classes. Mr. Albert C. Burrage, well known to New England horticulturists for his work with economic horticulture of garden vegetables, offered a delightfully informative course in Gardening with Vegetables. The course was highlighted by the instructor's pleasing personality as well as by his prejudices not only for good vegetables but for proper methods of preparation for the table. The course succeeded in tempting the palate as well as the mind. Dr. Karl Sax, of the Arboretum staff, offered a class in Plant Breeding which devoted several evening sessions to the genetic and morphological principles behind the practice of plant breeding and concluded with class meetings on the grounds where crosses were made of standard parentages and several others experimental in nature.

Mr. Coggeshall continued his classes in plant propagation with the second part of the course in the spring. Dr. Howard continued his class in plant identification as an advanced session working with the same group in field practice in late afternoon and evening sessions on the grounds of the Arboretum. A fifth class was Dr. Wyman's ever-popular spring field class, which was well attended.

In addition to the formal classes described, the staff joined in other types of instruction. During the spring, guided tours of the grounds were offered to any group bringing a minimum of twenty-five persons and scheduling the trip in advance. Garden clubs in particular are familiar with this service and use these trips as programs and sources of information. Few such trips end without a concentrated question-session.

The staff also cooperated with the Massachusetts Horticultural Society in presenting their annual Field Day at the Arnold Arboretum on Saturday, May 19th. Postcards to all members of the Horticultural Society announced the morning session which would consist of guided tours in sightseeing buses equipped with amplifiers to aid the guide in presenting his talk. The attendance was more than expected and the four buses were filled before the scheduled departure time, requiring additional guides for those who had to tour the grounds in their own cars.

This week would normally have seen the lilac collection at its peak and an open house on the Arboretum grounds was scheduled for the following Sunday, May 20th. However, the flowering season was delayed and crab apples, forsythia, magnolias and miscellaneous shrubs supplied the bloom then deficient in the lilacs. Staff members were stationed at strategic places throughout the Arboretum to give directions and to answer questions. It is of interest to note that on the afternoon of the open house the periphery of the Arboretum was completely outlined with parked cars.

Among the groups of visitors to the Arboretum was a study group of horticulturists and nurserymen from Europe. This group of well-known students of ornamental plants included seventeen Germans, one Austrian and one Swiss, with an American specialist as guide and interpreter. The staff was pleased to have these men visit the collections in Jamaica Plain

and regretted only that the close scheduling of their trip made their visit here of short duration.

One of the highlights of the year was the venture of the Arboretum staff into education by television. During the slack summer months the staff was invited to present a series of experimental programs on WGBH-TV Channel 2. The time was selected so that it did not conflict with important network shows and so that the staff of the television station could work closely with the novices in this field from the Arboretum staff. During July and August the Arnold Arboretum presented four weekly hour-long programs entitled "Notes from the Arnold Arboretum," prepared and presented by Mr. Coggeshall, Dr. Howard, Dr. Wood and Dr. Wyman. The staff was in agreement as to the excellence of the medium for presenting information about plants and the fine cooperation received from the studio technicians. However, each program required such a major effort in preparation that with the regular work program before the staff we reluctantly decided against further regular programs. Mr. Coggeshall, Dr. Wyman and Dr. Howard appeared, however, on feature programs or as guests on other programs such as "Discovery" and "Within Your Reach" during the winter and spring seasons. The staff individually and collectively received commendation for the programs and in turn extended their thanks to the cameramen and directors who presented plants in close-ups on television screens to the satisfaction and delight of all. The staff attempts to cooperate as fully as possible with the educational television station and kodachrome slides from the Arboretum collection appear regularly as background scenes for programs, while specimens and plant materials from the Arboretum collections have illustrated many other television programs.

Exhibits and Displays:

For the past several years the Arnold Arboretum has had an exhibit at the spring flower show of the Massachusetts Horticultural Society. During the past year considerable time and effort went into the preparation of an exhibit demonstrating methods of increasing plants. The exhibit on plant propagation covering 1200 square feet of floor space and developed under the direction of Dr. Wyman, Mr. Coggeshall, Mr. Williams and Mr. Howard, was an outstanding exhibit, which again won for the Arboretum a First Prize and a Gold Medal. One of the material aids the Arboretum received in preparing this exhibit was the use of a lean-to type of greenhouse lent through the courtesy of the New England Greenhouse Company, Inc., of Hanover, Massachusetts.

In the exhibit room at the Administration Building in Jamaica Plain the staff offered the annual show of Christmas plants and Christmas greens. In addition to the more common evergreens, the show displayed a collection of dried plant materials bought in advance from the florist markets in Boston. The correct botanical determination of these plants and some information about them was supplied on labels. An outstanding feature of the exhibit, however, was the wreaths and decorations made of dried fruits

FIG. 4. The Arboretum exhibit at the Spring Flower Show featured methods and materials for plant propagation. Designed and executed by Dr. Wyman, Mr. Coggeshall and Mr. Williams, the exhibit won a first prize and a gold medal.

FIG. 5. The Arboretum proudly acknowledges the salute of the Boston Envelope Company through this colorful reproduction of the Forest Hills Gate and the background plantings of cherries. This billboard along U.S. Highway No. 1 has brought many visitors and inquiries to the Arnold Arboretum.

and cones by Mrs. Donald Wyman. It is hoped to utilize the experience and materials of this portion of the exhibit in an issue of Arnoldia for the next Christmas season. A Christmas tree decorated with horticultural ornaments served as the focal point of this seasonal exhibit.

The open houses held at the Case Estates and at Jamaica Plain have been referred to elsewhere. As part of the Commencement Week activities, the staff held open house for members of the twenty-fifth reunion class in scheduling tours and demonstrations in the Harvard University Herbarium in Cambridge.

During the spring the Arboretum was honored with a colorful billboard display along U.S. Route 1. On a sign sponsored by the Boston Envelope Company and under the title, "The Boston Envelope Company salutes the Arnold Arboretum, America's Greatest Garden," there appeared a colorful reproduction of the Forest Hills Gate and the cherry and apple collections inside. As the sign is located at the junction of the Jamaicaway and Brookline Avenue and is illuminated at night, it drew many phone calls and sent additional visitors to the grounds this spring.

Library:

The librarian, Mrs. Lazella Schwarten, and her staff of regular and temporary help were active during the year in the organization and integration of the books housed in the Harvard University Herbarium Building. Work was divided between much-needed physical care of the bindings, changes in cataloguing and actual integration and was carried on in addition to regular services to staff, students and visitors. The air-conditioned and filtered environment has made easier the care of the library volumes. Thus bindings treated or replaced during the year show better retention of quality than ever before.

The integration and cataloguing work of the year concerned primarily the volumes of periodicals. Individual volumes and sets were compared and selected on the basis of condition, origin as gifts or autographed copies, as well as for annotations and usefulness. Complete active sets are now maintained and the duplicates are being held in reserve. The final selection of sets for current use required changes in cataloguing and listings on the volumes and in the main catalogue, the shelf-list cards and the Kardex guide. Lists are also maintained of the reserve volumes. The majority of periodicals are now shelved in one section of the stacks and as work proceeds on the monograph collections and some further shifting is done, the remaining periodicals will be placed in a planned sequence.

With the completion of work on the periodicals, efforts were directed to an examination of the monograph collection. It is planned to integrate and consolidate this collection from the Gray Herbarium and the Arnold Arboretum and the duplicates are to be shelved in the herbarium adjacent to the appropriate family. The monographs will be numbered according to the Dalla Torre and Harms system of Genera Siphonogarum with the Arnold Arboretum supplementary listings and the authors' numbers according to Cutter. This task was about seventy percent complete at the end of the fiscal year.

Changes were made in the section shelving of horticultural books housed in the Administration Building in Jamaica Plain. Portions of the library were shifted to the second floor along with the back numbers of periodicals to allow room for expansion in the main library room. The system of arrangement was changed, involving a complete shift of nearly all books in the library, but resulting in a more workable organization for those visitors not thoroughly familiar with the scientific classification of categories of books.

During the year three hundred books were added to the library, including forty-three specially selected books to complement the horticultural holdings. The total accessioned bound volumes is now 49,509. Pamphlets received and added to the library total two hundred eighteen numbers, making a grand total of 15,968. Five hundred catalogue cards were added to the main file, eight hundred shelf cards were prepared and one thousand cards were added to the Gray Herbarium species index.

Requests for books on inter-library loan continued high, numbering one

hundred thirty-six individual shipments during the year to all parts of the country. The librarian continues to assist where possible in supplying photocopies or microfilm reproductions. If the request is reasonable, the librarian often checks a reference or verifies a page or date in preference to sending a book on loan. Such services characterize and are a credit to our librarian.

During the year Mrs. Schwarten compiled six numbers of the Index to American Botanical Literature which is published in the Bulletin of the Torrey Botanical Club.

Dr. Frans Verdoorn, Research associate, gave most of his time to the preparation of a bibliographic guide to biohistory (the historical and other humanistic aspects of biology and medicine) with some special reference to botany and horticulture. Work on his biographical card index of plant scientists (Index Botanicorum), as well as the gathering of data for his annotated bibliographies on the history of botanic gardens and the Linnaean period was continued along the same lines as during previous years.

Herbarium:

The plans described in previous reports for the integration of the herbarium collections moved to Cambridge and housed in the Harvard University Herbarium were the basis for the work of most of the herbarium staff during the past year. The curator, Dr. Kobuski, directed the progress of the integration and by the end of the year considerable and very satisfactory progress had been made in placing the combined herbaria in first-class condition. During the past year the families of plants represented in the collections of the Gray Herbarium and the Arnold Arboretum which were in proximate arrangement received further adjustments. Two major steps are involved in the handling of each family. In the first step the component genera are placed in sequence and in the second step actual integration at the species or sub-species level is accomplished. Each of these moves may involve considerable work, but in small families both steps can often be accomplished in one operation. Old genus covers are replaced. New generic boards are prepared. Type or authentic specimens are separated. In large families such as the Leguminosae and Rosaceae, even the first step can be complicated and time-consuming. When both the Gray Herbarium and the Arnold Arboretum followed the same generic order and divisions, the task was mainly a physical one of shifting several thousand compartments of specimens. Where different generic order was used or where different generic concepts were recognized, the consistent organization of genera in successive order required careful planning and execution. The decisions to recognize segregate genera or where to place in sequence recently described genera were made after staff consultation so that all staff members taking part in the move were aware of the location and the treatments to be followed. A test case involved the family Verbenaceae, where all available staff members of both institutions, twelve in number, worked on one family at the same time to do complete integration. More

recent practice has been to work in teams of two individuals on the generic integration and as individuals on the species integration. Two workers, therefore, were able to shift and rearrange the genera of the Leguminosae with little confusion and little wasted effort after the initial decisions of generic limits were made and the work planned.

Integration within the genus involves the arrangement of species and subspecific units, the writing of new covers, the geographic arrangement and segregations and the selection and separation of type material. Type or authentic specimens are being placed at the end of the genus or generic geographic unit; e.g., Am. Bor., Ind. Occ., etc., and indication that the type has been removed is made in the species arrangement. Types are being placed in individual species folders for the first time.

Unidentified materials in the herbaria are placed where possible with the genus and the proper geographic unit. Material identified only to family is sorted geographically and filed at the end of the family. The arrangement of geographic areas for the Eastern Hemisphere is that followed by the Arnold Arboretum herbarium and the arrangement for areas of the Western Hemisphere (and particularly the United States) is that used by the Gray Herbarium. At the end of the year the rearrangement of over one hundred families was under way or was completed.

The fruit and seed collection and the photograph and negative collection received additional work during the year. Two college students were employed during the summer to continue the task of arranging the negatives and prints of the type and authentic specimens represented in our herbarium or photographed by staff members elsewhere. The fruit and seed collections were placed in boxes, rather than bottles, and are to be arranged in a system comparable to that used in the herbarium. The boxes of specimens will be stored in special trays and units on the first floor of the building where these collections will be equally available for use by the taxonomists of living plants and the students of the fossil seeds and fruits of paleobotany.

Work on the herbarium of cultivated plants has been limited to checking the coverage of the herbarium in relation to Rehder's Manual and other handbooks of cultivated plants and to mark and separate types of cultivated taxa and cultivars.

During the past year 6060 specimens were mounted and added to the herbarium, bringing the total accession count to 687,807 specimens in the Arnold Arboretum.

The herbarium of the Arnold Arboretum received during the year 19,850 specimens by gift, purchase or subsidy, and exchange. The vast majority of these, 16,599, represented the flora of Malaysia and Asia and 6056 of these were purchased by residual commitments. During the year the Arboretum sent out in continuation of exchange 23,460 specimens, of which nearly all went to herbaria and botanical gardens in Europe and Asia.

One of the major services which the Arboretum staff renders to the botanical and horticultural fields of research is the loaning of specimens from our herbarium. The large number of types and authentic specimens

in our herbarium indicates both the excellence of the collections and the activity of the staff members of the organization who have described new plants and placed in our herbarium the type specimen of the new unit. During the year the Arboretum received requests for the use of its material from forty-eight institutions in twelve different countries. Because of international or internal local disturbances and postal regulations, it was not possible to fill all of these requests. In total, eighty-seven loans were shipped out to forty-six institutions, half of them in the United States. The loans varied in size from single sheets to loans of 1498 and 1674 specimens. A total of over 14,000 specimens was sent out for the use and study of other students of plants.

The research activities of the herbarium staff were reduced again this year as the members devoted the majority of their time to work in the herbarium.

Dr. Howard worked on his collections of plants associated with bauxite soils from Jamaica and continued his studies of the genus *Coccoloba* in the West Indies. With the assistance of a technician, Miss Kathryn Greer, his research on the vascular structure of the petiole was expanded to include more tropical families and genera and involved some material from herbaria. Dr. Arthur Eames generously supplied for this study a large number of rare or unusual leaf forms, largely of the Proteaceae, from his collections of Australian plants.

Dr. Wood worked actively with the organization of a project on the flora of the Southeastern States. Along with Dr. Reed C. Rollins, director of the Gray Herbarium, he received support for this work through a three-year grant from the National Science Foundation. Surveys of bibliographies and indices are being made to classify recent literature references dealing with plants found in that area. Dr. Wood has continued his interest in the genera *Robinia* and *Drosera*, utilizing techniques of cytology and taxonomy in his study of each genus.

Dr. Channell, who has been working with Dr. Wood on the flora of the southeastern states, made a special study of the genus *Rynchospora*, as well as devoting a portion of his time to a completion of studies in progress of *Marshallia*.

Although much of his time is given to his regular work as editor of the Journal of the Arnold Arboretum and curator of the herbarium, Dr. Kobuski was able to devote a little time to the Theaceae, a family of his specialty.

Dr. Perry has accepted responsibilities for many phases of the work in the herbarium and was able to complete the preparation of labels for the collections made by L. J. Brass on the Fourth Archbold Expedition to New Guinea.

Mr. Canoso's work as curatorial assistant has been essential in the smooth functioning of the organization. During the year many collections have been received and accessioned. A major effort was the distribution of duplicate specimens on hand which had to be separated, packed and mailed.

The herbaria and the libraries have been used by the botanists working under the special grants for the Flora of China project. During the year Dr. Hu completed for publication a treatment of the Malvaceae and worked on an enumeration of the Compositae and the Orchidaceae of China. Dr. Liu worked on a monographic revision of the Pontederiaceae and the Stemonaceae for China and Dr. Hou completed revisions of the Palmae, Xyridaceae and Flagellariaceae for the same area.

Dr. Ivan Johnston continued his work on the Boraginaceae in Jamaica Plain and made one trip to Panama during the fall. During the spring semester Dr. Johnston was absent on sabbatical leave, dividing his time between Panama and the New York Botanical Garden.

Comparative Morphology:

Professor I. W. Bailey, Professor of Plant Anatomy *Emeritus*, has served voluntarily as the curator of the wood and pollen collection following his retirement. His efforts in arranging these collections and servicing requests for materials from the collections materially assisted the herbarium staff. Professor Bailey continues his anatomical studies and during the year completed several papers which will be published in the coming issues of the Journal of the Arnold Arboretum.

Several additions were made to the wood collection in the past year. The largest gift was a collection of wood samples from the forestry laboratory of British North Borneo. During the year Mr. Sherwin Carlquist, a National Science Foundation Fellow, studied the materials of the Compositae in the herbarium and the wood collection. Mr. Chen continued his interests in the anatomy of the Sapotaceae and utilized these collections and Dr. Abraham Fahn, visiting scholar from Hebrew University, Jerusalem, Israel, based his investigations on the Arnold Arboretum wood collections.

Cytogenetics:

Dr. Karl Sax, his assistants and students have reported the following contributions in the field of cytogenetics. It has been determined that the Sargent crab apple, *Malus sargentii* and its variety *rosea*, are facultatively apomictic. Some hybrids, however, have been obtained by crossing these plants with both ornamental and horticultural varieties of apple. The resulting hybrids are largely apomictic, suggesting that apomixis is a dominant character, at least in the hybrid swarms. If this is true, it should be possible to produce new varieties, both ornamental and economic in character, which can be reproduced from seed. Such work in selection continues.

Earlier interest in the species and varieties of lilacs has continued as crosses are made between *Syringa vulgaris* and *S. laciniata* and between *S. laciniata* and *S. pinnatifolia*. Both crosses have produced hybrids which are sterile. The sterility is apparently due to failure of the chromosomes to pair at meiosis. One possible method of overcoming this sterility barrier would be to increase the chromosome number and the production of arti-

ficial polyploids is being attempted with the use of colchicine. One induced tetraploid of *Syringa vulgaris* has been produced and has flowered, but so far has failed to set seed when crossed with other clones.

The use of bark inversions to alter the shape and flowering or fruiting characteristics of ornamental and economic trees remains a portion of the research interests of Dr. Sax. The antiquity of this field of research was the subject of an interesting article by Dr. Sax which appeared in the National Horticultural Magazine and was entitled, "What is New in Plant Propagation?" The technique of bark inversion has demonstrated that earlier flowering can be induced by inverting a ring of bark or by tying a knot in the stem of young plants of clonal vegetative propagated varieties. The techniques do not induce earlier flowering in seedlings and as yet no way has been found to shorten the juvenile stage of seedling trees.

Additional grants have been awarded to Dr. Sax by the Atomic Energy Commission to support research in basic investigations of chromosomal structure and behavior. A study of X-ray-induced chromosome aberrations financed by these grants has indicated that the chromosomes become bipartite a full generation before the daughter chromosomes divide. Dr. Sax has also worked in collaboration with the scientists and directors of the Gamma-radiation field at the Brookhaven National Laboratories. The ornamental plants from the Arnold Arboretum which have been grown in this radiation field have not shown as yet any recognizable mutations.

Instruction:

No regularly scheduled classes were offered by staff members during the year, although several took part in seminars and presented lectures for students in areas of their specialties. Two of Dr. Sax's former students completed their theses which were submitted and approved. On the basis of their work Dexter Sampson, now in the Department of Horticulture of the Ottawa Experimental Farm in Ottawa, Canada, and Gweneth Carson, currently a cytologist at the University of California, were awarded the degree of Doctor of Philosophy. Dr. Sax supervised the work of Mr. Claude Brown on bark regeneration and of Frank Santamour who is working on polyploidy in *Populus*. Mr. Tchang Bok Lee, a UNKRA fellow from Korea, continued his graduate work under the guidance of Dr. Howard and instigated during the spring work in hybridization of Korean and North American oaks in the Arboretum collection.

In the regularly scheduled seminars held at the Harvard University Herbarium, the Arboretum staff members contributed several programs. During the spring semester Dr. Wood talked about the "International Rules of Botanical Nomenclature" and was assisted by Dr. Perry; Dr. Howard spoke on the problems and practices of "Nomenclature of Cultivated Plants" and Dr. Kobuski and Dr. Hu reviewed the status of published and unpublished floras for the Eastern Hemisphere.

During the fall semester the seminar was devoted to a consideration of the vegetation of the southeastern states and the associated problems involved in a study of this area. Dr. Wood discussed the geology and geog-

raphy of the area, while Dr. Channell and Dr. Howard discussed two aspects of the vegetational relationships in the area. Dr. Hou also took part in this seminar series and reported on his work with *Celastrus* as an example of methods of study and vegetational relationships.

Travel and Exploration:

The Arboretum continued the policy of supporting its own staff members and other reliable collectors in field work and botanical exploration and collecting. A grant from the American Association for the Advancement of Science, through the American Academy of Arts and Sciences, enabled Dr. Wood to continue a study of the sundews in the Gaspé region of Canada and in northern Michigan. During the spring Dr. Wood collected additional woody materials for trial and study in the southeastern United States. Miss Kathryn Greer, assistant to Dr. Howard, collected morphological materials for anatomical studies in Cuba by means of special funds awarded to Dr. Howard by the American Philosophical Society. Dr. Howard made two short trips to Jamaica to further his study of the vegetation on bauxite soils and the replacement of vegetation on mined-out bauxite pits. During one trip he was able to join botanists from the Institute of Jamaica in an exploratory trip into the John Crow mountains at the eastern end of the island. This mountain range represents the largest and perhaps the most difficult unexplored area left in Jamaica. The goal of this exploration party was to locate a possible site for a base camp having reliable sources of water for further biological exploration of this important mountain chain. Such an area was located and it is hoped that the camp site can be developed for use by naturalists during the next few years.

Dr. Ivan Johnston made one collecting trip to Panama on contract with the U.S. Army Engineers during the fall and did extended work in the same area during a sabbatical leave of absence in the spring semester. His botanical collections from this rain forest will supplement those he made on San José Island of Panama during the war years.

During the spring the Fifth Archbold Expedition, under the direction of Mr. Leonard J. Brass, left for field work in New Guinea. The staff of the Arboretum, under Dr. Merrill's directorship, assumed full responsibility for the identification of the botanical materials from the second, third and fourth expeditions. However, since identifications for the botanical collections of the fourth expedition are not yet completed, the Arboretum agreed only to assist financially this fifth expedition in exchange for one of the early sets of materials.

Gifts and Grants:

The annual appeal to the Friends of the Arnold Arboretum was issued during the spring of the year and the generous gifts indicated the enthusiastic support of the public. The director and his staff are grateful for the gifts from the Friends which are unrestricted and used for horticultural work on the grounds and in our laboratories. During the past year

such gifts made possible a research assistant in the field of cytogenetics, additional help in the greenhouses for plant propagation and labor on the grounds to assist in cleaning and trimming along the paths and roads. Special gifts were also received from Friends for the support of collecting plant specimens and for the publication of writings by staff members.

Again during this year the largest single gift was received from the trustees of the China International Foundation for the support of work on the Flora of China carried on by Drs. Hu, Liu and Hou. Dr. Sax received additional grants from the Atomic Energy Commission for the support of his research and Dr. Howard received a grant from the American Philosophical Society to continue his investigations on the vascular structure of the petiole of higher plants. An additional non-departmental gift from Mr. George R. Cooley for taxonomic work at the joint discretion of Drs. Rollins and Howard was used to support field work and research on the vegetation of the southeastern United States.

We particularly appreciate the kindness of Mrs. Oakes Ames in giving permission to have reproduced her drawing of *Davidia involucrata*. Copies of this excellent print, suitable for framing, have been sent to the Friends of the Arnold Arboretum in acknowledgment of their gifts.

Gifts in kind were numerous and equally appreciated. Gift volumes for the library were received from several sources and included a fine set of Louden's Botanical Encyclopedia of 1854 in excellent bindings presented by Mrs. Frederic Goodwin. The Arboretum received many gifts of plant materials from organizations with which we regularly trade material and information and in addition received noteworthy gifts of material from individuals. Among these latter were cuttings of dogwood received from Miss Harriet R. Halloway, nine scions of tree peonies, originations of Dr. A. P. Saunders, from Miss Silvia Saunders and a group of seven rare evergreens from Mr. Robert E. More.

Publications:

Special attention should be directed to the publications of the staff which have appeared during the past year. Mrs. Susan D. McKelvey, research associate of the Arnold Arboretum and long a member of the Committee to Visit the Arnold Arboretum, completed the work on the proofs of her latest book and saw the first copy issued on March 26, 1956. The book is entitled "Botanical Exploration of the Trans-Mississippi West 1790–1850" and represents long and meticulous research in checking the routes and the botanical collections of the men of science who assisted in opening up the West. Mrs. McKelvey's book contains several excellent maps drawn by Dr. Erwin Raisz. It was published by the Arnold Arboretum and was printed by the Anthoensen Press of Portland, Maine.

Dr. Sax's book entitled "Standing Room Only" was published by the Beacon Press during the year and has been widely reviewed and discussed as a continuing contribution to demographic study.

In March the Macmillan Company issued Dr. Donald Wyman's latest book, "Ground Cover Plants." This book contains 175 pages, is profusely

illustrated and is unique as a record of experience in growing ground cover plants. Also during the year the revised edition of "Crab Apples for America" was published by the American Association of Botanical Gardens and Arboretums. Dr. Wyman was chairman of the committee which compiled the data and was responsible for its publication.

Three issues of the Journal of the Arnold Arboretum were published under the editorship of Dr. C. E. Kobuski. The fourth number of this magazine, which is normally a quarterly, was issued as a double number dedicated to Professor I. W. Bailey during the previous fiscal year. Twelve numbers of Arnoldia were published and issued as seven units, two of which were combined numbers. These were "Christmas Plants for the Boston Area" and the Arboretum's "Spring Planting Notes."

A sample treatment of the Malvaceae was issued on behalf of the Flora of China project. This monographic treatment of the family was written by Dr. Hu and printed by the Tudor Press. In 1953 Dr. Hu was awarded first prize in a Project Suggestion Contest sponsored by the Continental Development Foundation. The problems of preparing a flora of China was the subject of Dr. Hu's essay and the suggestion was considered by the committee to be worthy of further support. With grants from the China International Foundation, work was begun as proposed in the essay, using the library and herbarium resources of the Arnold Arboretum to compile in card catalogue form data on the occurrence, distribution and publication of vascular flowering plants of China. This card catalogue represents the most complete and up-to-date catalogue of vegetational records for the Asiatic mainland and will serve as the basis for future work in forestry, horticulture, floristics and agriculture. The catalogue is available for the use of all qualified visitors to the Arboretum and requests for information from other areas will be filled by photocopy or typescript at cost. To demonstrate the type of work which can be done using these cards and as a possible format for future publications towards a flora of China, Dr. Hu prepared the recently published treatment of the Malvaceae. It is hoped that other botanists will utilize the card resources made possible by the generosity of the trustees of the China International Foundation and that additional family treatments can be published as manuscript and funds are available.

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1955–1956

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